U.S. Department
of Commerce

Volume 113
Number 1
January 2015

Fishery Bulletin

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The *Fishery Bulletin* (ISSN 0090-0656) is published quarterly by the Scientific Publications Office, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

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U.S. Department of Commerce
Seattle, Washington

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Fishery Bulletin
established 1881

Spencer F. Baird
First U.S. Commissioner
of Fisheries and founder
of *Fishery Bulletin*

Seasonal movement patterns and temperature profiles of adult white seabass (*Atractoscion nobilis*) off California

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Abstract—To better understand the seasonal movement patterns of adult white seabass (*Atractoscion nobilis*), 173 depth- and temperature-sensitive data storage tags were deployed at various sites within the Southern California Bight during 2008–2011. Commercial and recreational fishing crews recaptured 41 tagged individuals (24%) between La Salina, Baja California Norte, Mexico (32°01′N, 116°53′W), and Half Moon Bay, California (37°28′N, 122°28′W). Tagged fish were at liberty for an average duration of 468 days (range: 9–1572 days), and mean net displacement between the points of release and recapture was 229 km (range: 2–624 km). Collectively, 9130 days of archived data revealed distinct seasonal trends in depth distribution, and significantly deeper profiles during the winter months. Minor differences in mean depth values were evident between daytime (14.9 m [±standard deviation (SD) 5.1]), nighttime (15.5 m [SD 5.1]), and twilight periods (16.8 m [SD 6.8]). However, the vertical rate of movement (VROM) was significantly greater during twilight hours (48.9 m h^{-1} [SD 12.3] when compared with day and night VROM values (39.6 m h^{-1} [SD 10.8] and 41.1 m h^{-1} [SD 13.2]). The greatest depth achieved by any individual was 245 m; however, 95% of all depth records were less than 50 m. Ambient water temperatures ranged from 8.7° to 23.6°C, and had a mean value of 15.2°C (SD 1.4°C). A vertical shift toward the surface as water temperatures increase during the spring and summer months contributes to heightened vulnerability during the spawning season, presenting management challenges toward the long-term sustainability of this resource.

Manuscript submitted 13 August 2013.
Manuscript accepted 27 October 2014.
Fish. Bull. 113:1–14 (2015).
doi: 10.7755/FB.113.1.1

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

The white seabass (*Atractoscion nobilis*) supports lucrative recreational and commercial fisheries throughout California and Baja California, Mexico (Vojkovich and Crooke, 2001; Rosales-Casian and Gonzalez-Camacho, 2003). Because of their high recreational and market value, white seabass are targeted opportunistically and fishing effort is influenced by local availability (Skogsberg, 1939; MacCall et al., 1976; CDFG, 2011). During periods of heightened abundance, persistent localized effort is directed toward white seabass by both recreational and commercial operations throughout much of the range of this species (Whitehead, 1929; MacCall et al., 1976).

Over the past century, landings and catch per unit of effort (CPUE) of white seabass in California have fluctuated dramatically, reaching peak levels in the early 1920s and late 1950s that were followed by troughs in the late 1920s and 1960s (Whitehead, 1929; MacCall et al., 1976; CDFG[1]). Vojkovich and Reed (1983) suggested that prolonged intervals of reduced landings off California are likely a response to periods of overexploitation and other unknown factors. Collective landings and CPUE from California recreational and commercial fisheries have steadily increased since 1998, indicating a recent stock resurgence from levels of record-low abundance in the 1980s (Vojkovich and Reed, 1983; Allen et al., 2007; CDFG, 2011).

The majority of California's white seabass harvest typically occurs from April to September along the southern coast from Point Conception to San Diego and throughout the Channel Islands (Skogsberg, 1925; Thomas, 1968). Landings north of Point Conception have increased dramatically since 2008; commercial hook-and-line catches north of Point Arguello increased from 1% of the total California harvest in 2008 to 22% of annual state landings in 2010 (CDFG, 2009; 2011). Over the same period, recreational catches north of Point Arguello increased from 3% to 38% of total state landings. Heightened landings from the northern region have been coupled with a sharp increase (266%) in the numbers of vessels entering the white seabass fishery (CDFG 2011), rising from 93 permitted boats in 2009 to 254 commercial vessels in 2011 (CDFG[2]). A

[1] CDFG (Calif. Dep. Fish Game). 2002. Final white seabass fishery management plan (WSFMP), 161 p. [Available from https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=34195&inline=true, accessed March 2014.]

[2] CDFG (Calif. Dep. Fish Game). 2012. White seabass fishery management plan annual 2010–2011 review, 6 p. [Available from https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=75302&inline=true, accessed March 2014.]

comparable northward shift in fishing effort was documented from 1957 to 1961 and was also coupled with a sharp increase in the number of vessels that entered the fishery (Vojkovich and Reed, 1983). During this period, commercial landings of white seabass reached a record high of more than 1500 metric tons in 1959, 36% of which came from the waters north of Point Conception (Thomas, 1968; Vojkovich and Reed, 1983). Interannual shifts in the latitudinal distribution of white seabass have been suggested in the past (Skogsberg, 1939; Young[3]; Maxwell[4]); however, fishery-independent data on movement patterns and stock structure of white seabass have been limited.

Attempts to evaluate movement patterns of juvenile white seabass through a conventional tagging program in the mid-1970s were ineffective because of limited tag deployments (n=58) and no reported tag recoveries (Maxwell[4]). An evaluation of movement patterns based on historical fishery data indicates that white seabass occur off Baja California during winter and move northward along the coast of California as water temperatures increase during the spring and summer months (Skogsberg, 1939; Maxwell[4]; Vojkovich and Crooke, 2001). Spawning is thought to occur with northward advancement from March to July (Skogsberg, 1925; Thomas, 1968; Young[3]), although little information is available regarding spawning activity north of Point Conception. Fish harvested along California and Baja California are currently considered to be from a continuous spawning population with a high level of genetic diversity (Maxwell[4]; Coykendall, 1998; Rios-Medina, 2008). Discrepancies in this single-stock model have been indicated by Franklin (1997), and the existence of regionally discrete stocks with limited rates of mixing has been considered (Vojkovich and Crooke, 2001).

Despite a robust history of white seabass catch data since the 1890s, essential fishery information on the geographic distribution of stocks, habitat use, and seasonal movement patterns remains largely unavailable (Skogsberg, 1939; Vojkovich and Reed, 1983; CDFG[1]). Additional uncertainties on spatial and temporal aspects of white seabass depth distribution, residence periods, and exploitation rates present major challenges for effective fishery management, particularly for a population that is harvested by more than one nation (Thomas, 1968; Maxwell[4]; CDFG[1]). Regulations that reduce the likelihood of overexploitation are currently in place; however, additional research and adaptive management strategies are necessary for the sustainable use of this valuable fishery resource (Vojkovich and Reed, 1983; CDFG[1]). Fishery-independent information on fine- and course-scale fish movements has been identified as essential to adequately assess fishery impacts and address questions related to seasonal distribution and stock structure of white seabass (Thomas, 1968; CDFG[1]). Our objectives were to assess movement patterns, temperature preferences, and recapture rates of adult white seabass off the California coast.

Materials and methods

Tagging procedure and sampling regime

Cefas G5[5] and G5 long-life data storage tags (DSTs; Cefas Technology Limited, Lowestoft, UK) were surgically implanted in the peritoneal cavity of white seabass by using techniques modified from Stutzer (2004). Wild-caught white seabass were tagged and released around Santa Catalina Island (n=107) and along the southern coastline of California (n=66) during the spring and summer months of 2008–2011 (Table 1). After capture on hook and line, fish were brought alongside the vessel and transferred in a knotless nylon-mesh dip net (Duraframe, Viola, WI) to an onboard tagging cradle. A conventional identification marker (FIM-96; Floy Tag, Inc., Seattle, WA) was inserted into the dorsal musculature traversing the dorsal-fin pterygiophores. Upon securing the fish ventral-side up within a tagging cradle, a 2-cm incision was made with a scalpel through the dermal layer adjacent to the ventral midline approximately 8 cm anterior to the anal vent. A stainless steel trocar was used to penetrate the ventral musculature, and a DST was inserted into the peritoneal cavity. The incision was closed around an external identification stalk with a PDS II surgical-grade suture and a CP-1 reverse cutting needle (Ethicon, Somerville, NJ) along with a 35-wide stainless-steel skin stapler (PGX-35W; 3M, St. Paul, MN).

Fish total length (TL) was measured to the nearest centimeter, sex was recorded, and the hook was removed before release. Sex was determined by both the audible detection of low-frequency sound production by males during the capture and tagging process and the presence or absence of milt upon application of pressure to the abdominal region. All tagging was conducted during the spawning season when mature males are consistently running ripe and characteristically produce low-frequency sound upon handling (Aalbers and Drawbridge, 2008; Gruenthal and Drawbridge, 2012). Total handling time onboard the vessel ranged from 65 to 135 s.

Because postrelease survival of white seabass hooked in the visceral region has been shown to be

[3] Young, P. H. 1973. The status of the white seabass resource and its management. Calif. Dep. Fish Game Mar. Resour. Tech. Rep. 15, 10 p. [Available from http://aquaticcommons.org/756/1/Technical_Report_1973_No._15_A.pdf, accessed April 2014.]

[4] Maxwell, W. D. 1977. Progress report of research on white seabass, *Cynoscion nobilis*. Calif. Dep. Fish Game Mar. Resour. Admin. Rep. 77-14, 14 p. [Available from http://aquaticcommons.org/76/1/Marine_Resources_Administrative_Report_No[1]._77-14.pdf, accessed April 2014.]

[5] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Tag deployment and recovery statistics for 41 adult white seabass (*Atractoscion nobilis*) recaptured between La Salina, Baja California Norte, Mexico, and Half Moon Bay, California, from June 2008 to July 2013. DAL=days at liberty, rec. hook-line=recreational hook and line, com. hook-line=commercial hook and line.

Tag no.	Fish total length	Deployment			DAL	Recapture			Net movement	Recapture gear
		Date	Latitude	Longitude		Date	Latitude	Longitude		
A02049	132 cm	5-19-08	33°18′ N	118°18′ W	1154	7-18-11	33°20′ N	118°29′ W	16 km	rec. hook-line
A02066	127 cm	5-19-08	33°18′ N	118°18′ W	1572	9-11-12	36°57′ N	121°57′ W	542 km	com. hook-line
A02055	119 cm	5-25-08	33°18′ N	118°18′ W	767	6-30-10	34°13′ N	119°20′ W	144 km	U.S. gill net
A02071	114 cm	5-25-08	33°18′ N	118°22′ W	31	6-25-08	34°14′ N	119°25′ W	144 km	U.S. gill net
A02143	97 cm	6-02-08	33°28′ N	118°36′ W	798	8-10-10	37°28′ N	122°28′ W	624 km	com. hook-line
A02054	124 cm	6-12-08	33°18′ N	118°18′ W	746	6-28-10	33°39′ N	118°12′ W	40 km	U.S. gill net
A02118	117 cm	6-12-08	33°18′ N	118°18′ W	1342	2-13-12	34°18′ N	119°27′ W	211 km	U.S. gill net
A02119	117 cm	6-12-08	33°18′ N	118°18′ W	377	6-24-09	33°40′ N	118°13′ W	19 km	rec. hook-line
A02159	119 cm	6-12-08	33°18′ N	118°18′ W	764	7-26-10	34°00′ N	118°48′ W	90 km	speargun
A02075	91 cm	6-26-08	33°18′ N	118°21′ W	371	6-30-09	34°14′ N	119°19′ W	125 km	U.S. gill net
A02105	122 cm	7-15-08	33°18′ N	118°21′ W	350	6-29-09	34°12′ N	119°19′ W	141 km	U.S. gill net
A02131	109 cm	5-06-09	33°24′ N	118°22′ W	76	7-21-09	36°58′ N	121°56′ W	576 km	rec. hook-line
A03604	152 cm	5-14-09	33°18′ N	118°21′ W	690	4-06-11	32°01′ N	116°53′ W	195 km	Mexico gill net
A02128	127 cm	6-05-09	33°24′ N	118°22′ W	896	11-21-11	36°58′ N	122°08′ W	600 km	com. hook-line
A03606	114 cm	6-08-09	33°18′ N	118°21′ W	490	10-12-10	36°37′ N	121°52′ W	512 km	com. hook-line
A03609	124 cm	6-16-09	33°18′ N	118°20′ W	741	6-27-11	33°40′ N	118°12′ W	45 km	U.S. gill net
A03613	79 cm	6-23-09	33°18′ N	118°21′ W	16	9-07-09	33°19′ N	118°25′ W	11 km	rec. hook-line
A02094	102 cm	6-29-09	33°20′ N	117°34′ W	820	9-27-11	32°01′ N	116°53′ W	192 km	Mexico gill net
A02325	112 cm	6-29-09	33°20′ N	117°34′ W	354	6-18-10	33°39′ N	118°12′ W	45 km	U.S. gillnet
A02161	132 cm	6-30-09	33°20′ N	117°34′ W	744	7-14-11	34°24′ N	119°49′ W	237 km	speargun
A03595	122 cm	7-09-09	33°20′ N	117°34′ W	722	7-01-11	33°17′ N	117°29′ W	6 km	speargun
A03596	124 cm	7-10-09	33°20′ N	117°34′ W	439	9-22-10	36°37′ N	121°54′ W	587 km	com. hook-line
A03591	152 cm	7-18-09	33°23′ N	117°37′ W	346	6-28-10	32°47′ N	117°17′ W	72 km	com. hook-line
A02109	109 cm	3-16-10	32°50′ N	117°18′ W	146	8-08-10	35°06′ N	120°39′ W	448 km	com. hook-line
A02111	104 cm	3-17-10	32°50′ N	117°18′ W	153	8-15-10	32°51′ N	117°18′ W	2 km	rec hook-line
A02133	114 cm	3-17-10	32°50′ N	117°18′ W	493	7-24-11	32°09′ N	116°54′ W	86 km	Mexico gill net
A06101	124 cm	5-05-10	33°17′ N	117°29′ W	17	5-22-10	32°51′ N	117°17′ W	56 km	speargun
A06097	135 cm	5-20-10	33°20′ N	117°34′ W	416	7-10-11	36°57′ N	121°57′ W	602 km	com. hook-line
A06065	137 cm	5-26-10	33°18′ N	118°22′ W	27	6-22-10	33°39′ N	118°15′ W	45 km	U.S. gill net
A06089	86 cm	5-26-10	33°19′ N	118°23′ W	386	6-16-11	34°13′ N	119°26′ W	120 km	U.S. gill net
A06101b	140 cm	5-26-10	33°18′ N	118°22′ W	155	10-28-10	36°37′ N	121°52′ W	520 km	com. hook-line
A06067	114 cm	5-27-10	33°18′ N	118°22′ W	97	8-31-10	36°32′ N	121°56′ W	506 km	com. hook-line
A06076	117 cm	5-27-10	33°18′ N	118°22′ W	385	6-16-11	34°15′ N	119°20′ W	120 km	U.S. gill net
A06117	130 cm	6-12-10	33°36′ N	117°58′ W	106	9-26-10	36°37′ N	121°52′ W	552 km	com. hook-line
A06122	104 cm	6-12-10	33°36′ N	117°58′ W	11	6-23-10	33°40′ N	118°17′ W	32 km	U.S. gill net
A06118	102 cm	6-13-10	33°36′ N	117°58′ W	8	6-22-10	33°39′ N	118°16′ W	29 km	U.S. gill net
A06120	130 cm	6-13-10	33°36′ N	117°58′ W	765	7-18-12	36°57′ N	121°57′ W	568 km	com. hook-line
A06107	130 cm	6-24-10	32°47′ N	117°17′ W	355	6-14-11	32°42′ N	117°16′ W	8 km	speargun
A06073	91 cm	6-07-11	33°18′ N	118°20′ W	110	9-24-11	33°23′ N	118°29′ W	19 km	speargun
A02143	127 cm	3-17-10	32°50′ N	117°18′ W	1155	5-17-13	32°42′ N	117°16′ W	12 km	speargun
A06108	135 cm	6-25-10	32°47′ N	117°17′ W	695	7-17-13	32°42′ N	117°16′ W	11 km	com. hook-line

compromised (Aalbers et al., 2004), only mouth-hooked individuals in good physical condition (e.g., no hook damage) were selected for tagging. Fish were captured at depths of 3–33 m. Most individuals were positively buoyant upon capture as a result of gas bladder expansion; however, artificial deflation of the gas bladder was unnecessary, and all tagged fish were able to return to depth after release.

Contact and reward information was printed upon both the stalk and body of the DSTs as well as on externally affixed conventional tags. Information on recapture vessel, geographic location, fish size, sex, and general fish condition was documented upon communication with fishermen that reported tag recoveries. A $200 reward, tagging project T-shirt, and a summary of statistics for the recaptured individual were sent out to fishermen upon recovery of a DST.

DSTs were programmed by using 3 sampling re-

gimes to maximize fine-scale data acquisition within the constraints of tag memory capacity and battery life. In 2008, Cefas G5 DSTs were programmed to record depth (0.15 m resolution) every 2 min and temperature (0.1°C resolution) every 4 min. In 2009, Cefas G5 long-life DSTs stored depth and temperature records every 2 min, and tags in 2010 recorded depth at 1-min intervals and temperature every 2 min. Time-series data for cumulative analyses were standardized to a sampling regime of 2-min intervals for depth and 4-min intervals for temperature for all tag recoveries.

Upon recovery, fine-scale depth and temperature data were downloaded from all DSTs and complete time-series records over the entire deployment period were recovered from 22 DSTs. Battery life expired before recovery of 11 DSTs; however, the time-series data for the active recording life of these 11 DSTs were retrieved and provided by the tag manufacturer (Cefas Technology Limited). Four of the internally implanted DSTs were either shed through the incision site or incidentally discarded along with the viscera during fish processing, as only conventional identification markers were reported by fishermen. Subsequent investigations should incorporate 3 recovered data sets because recaptures were reported after completion of comprehensive data analyses, and 1 DST was lost in the mail.

Data analysis

Time-series data were formatted in Excel worksheets before export into an Access database (Microsoft Office 2010, Redmond, WA). All records were classified as *day*, *night*, or *twilight* values on the basis of the mean monthly time (Pacific Standard Time [PST]) of sunrise, sunset, and nautical twilight at the initial tagging location from the Astronomical Applications Department of the U.S. Naval Observatory data services portal (http://aa.usno.navy.mil/data/index.php). Daytime was defined as the average monthly time of sunrise until the average time of sunset; nighttime was assigned to all values between the mean time of nautical twilight at dusk until the mean time of nautical twilight at dawn; and twilight values included all data between mean time of sunset and nautical twilight at dusk as well as from nautical twilight at dawn until mean time of sunrise for each month.

Vertical rate of movement (VROM) was calculated for each fish (n=33) as the absolute difference of all subsequent records of depths taken every 2 min. Individual VROM values were converted to m h^{-1} before subsequent analyses. For all fish, VROM values that exceeded 150 m h^{-1} were binned by hour of the day to further evaluate daily periods of peak vertical activity. Depth values ≤5 m were binned by month and by hour to identify periods of surface-oriented behavior. Analyses did not control for autocorrelation in the mean comparisons and descriptive statistics used to characterize vertical data by time of day and season.

Seasonal depth statistics were evaluated for the 16 individual fish for which time-series data was collected for each month of the calendar year. Daily depth and temperature means were calculated and plotted with a 7-day running mean for smoothing. Daily depth probability plots were constructed with Matlab software vers. 6.0 [R12] (The MathWorks, Inc., Natick, MA) for each month with depth bins of 1 h by 2 m to illustrate the cumulative probability of occurrence for each depth. Spectral analysis by use of the fast Fourier transform (FFT) algorithm was conducted to show the diurnal signal and associated harmonics dominating in the frequency range of 0.5–8.0 cycles per day (cpd), and a Hanning window was used to reduce overlap between adjacent spectral peaks (Shepard et al., 2006). Data on mean daily depths were used to remove the diurnal cycle before long-period oscillations in the frequency band of 0.02–0.14 cpd were calculated for the 3 longest time series (721–741 days).

A paired t-test was conducted from mean depth values of 16 data sets that contained time-series records for each month of the calendar year to determine if seasonal differences were apparent between winter months (October–March) and summer months (April–September). Paired t-tests were also employed for all white seabass (n=33) to identify differences in VROM values: daytime versus nighttime periods, daytime versus twilight periods, and nighttime versus twilight periods. All mean values are indicated as means with standard deviations (SD) in parentheses, and $\alpha<0.05$ was used to infer significance.

Results

Tag deployments and recoveries

Between April 24, 2008, and June 8, 2011, 173 adult white seabass, ranging in size from 71 to 152 cm TL (mean=118 cm TL), were affixed with DSTs. Of the 95 individuals for which sex was determined during tagging, 76% were identified as females and 24% were sound-producing males. Commercial and recreational crews recaptured 41 tagged individuals (77% female) during the study period, an overall recapture rate of 24% (Table 1). Annual recapture rates varied from a low of 6% (1 of 17) for 2011 deployments to a high of 29% (17 of 58) for 2010 deployments. Collectively, the largest number of tag recoveries also occurred in 2010, with 17 of the 41 tag recoveries (41%) reported during that year. Between the months of April and October, 95% of tag recaptures occurred. Of the 41 recaptured individuals, 13 were harvested by California gillnetters, 3 were reported by Mexican gillnetters, 13 were taken by California commercial hook-and-line vessels, 5 were caught by California recreational anglers, and 7 were recovered by California spear fishermen (Table 1).

Collectively, 9130 days of time-series data compiled from 33 DSTs provided 6.30×10^6 depth and 3.65×10^6

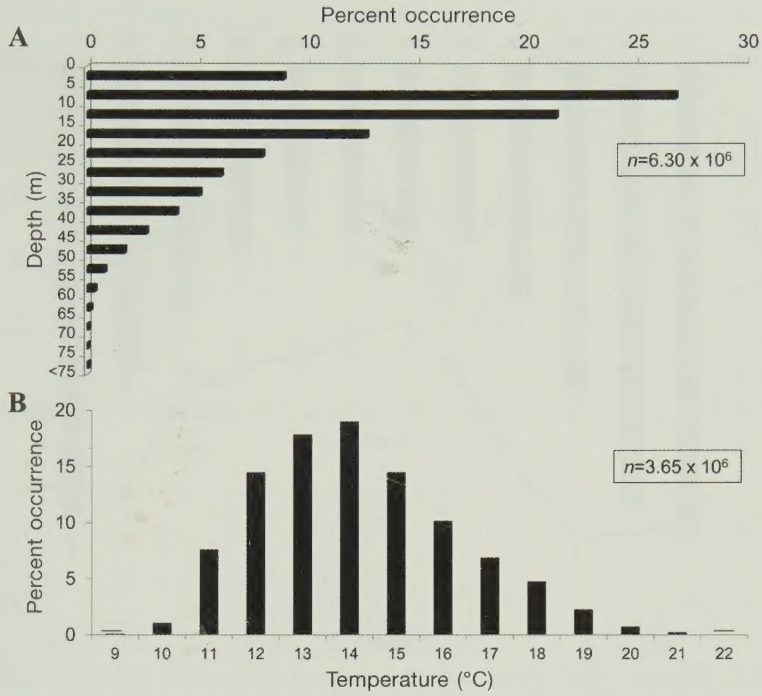

Figure 1

Frequency distributions showing collective (**A**) depth and (**B**) temperature profiles for 33 adult white seabass (*Atractoscion nobilis*) that were tagged and recaptured along the California and Baja California, Mexico, coastlines during 2008–2011. Observations are based on depth bins of 5 m by 2 min and temperature bins of 1°C by 4 min.

temperature records at resolutions of 2 min and 4 min. Fish at liberty for periods of up to 1572 days (mean=468 days) provided comprehensive multiyear data sets for an evaluation of seasonal and interannual patterns of depth distribution and habitat use.

Vertical movements

The cumulative mean depths during the daytime, nighttime, and twilight periods were 14.9 m (SD 5.1), 15.5 m (SD 5.1), and 16.8 m (SD 6.8), respectively. Brief vertical excursions to depths up to 245 m were recorded; however, 95% of all the recorded depths were <50 m (Fig. 1A). Monthly mean depth values of tagged fish revealed that the fish remained significantly deeper in the water column between October and March (paired *t*-test: t=14.41, P<0.0001) than between April and September, reaching a maximum mean depth of 31.1 m (SD 13.2) in January (Fig. 2). Depth profiles were shallower on average as water temperatures increased during the spring and summer months, reaching a minimum mean depth of 10.5 m (SD 7.3) in August (Fig. 2).

Although diel and seasonal depth patterns were consistent among most fish, individual variability and interannual trends were apparent from mean daily depth and temperature profiles (Fig. 3, A and B). For example, fish A06097 remained consistently deeper (27.0 m [SD 13.5]) than all other white seabass (9.4 m [SD 4.5], n=4) during the summer months of 2010. In comparison, fish A03591 occurred at roughly half (14.4 m [SD 3.7]) of the mean depth observed for all other fish (28.9 m [SD 4.5], n=7) during the winter months of 2009–2010. Although A03591 was the largest female (152 cm TL) tagged during this study, a consistent correlation was not found between fish size and mean depth, fish size and mean temperature, or sex and mean depth. Mean depth and temperature from August to October in 2010 were considerably less for 5 individuals recaptured within Monterey Bay than for all other fish recaptured in other areas: 8.7 m and 13.6°C versus 13.0 m and 15.4°C.

Depth probability plots constructed for each month represented seasonal shifts in depth, indicating more surface-oriented distributions evident from April to October, transitional periods during March and November, and deeper profiles from December to February (Fig. 4, A–D). Fish showed more of a bimodal depth distribution during transitional periods, with peaks in cumulative probability near 10 m as well as at depths between 15 and 30 m (Fig. 4, B and D).

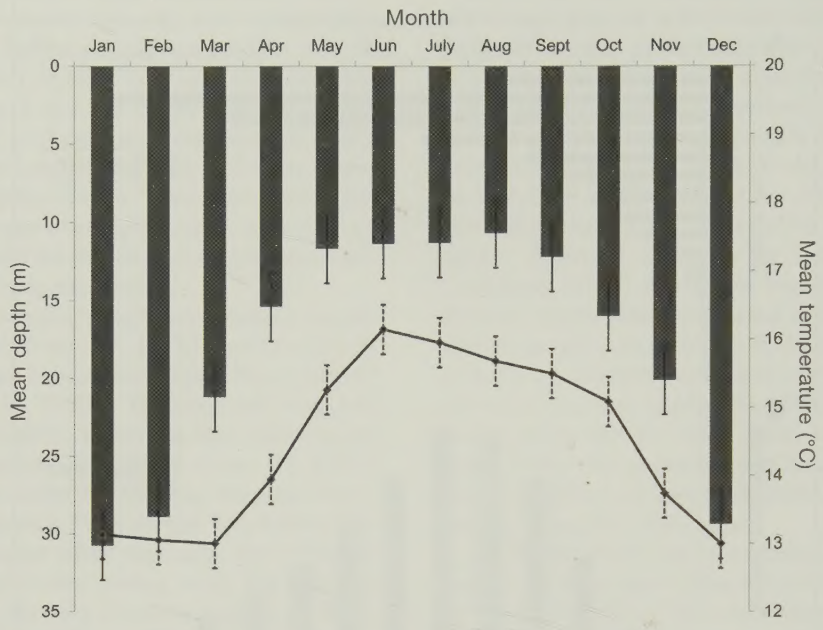

Figure 2

Mean seasonal depth (bars) and temperature (line) profiles from time-series records of 16 wild-caught white seabass (*Atractoscion nobilis*) at liberty along the coast of California and Baja California, Mexico, throughout all months of the year. Collectively, the time-series data span from May 2008 to June 2011. Error bars indicate ±1 standard error of the mean.

Depth probability plots summarized for 16 fish over a 24-h period also exhibited increased vertical activity around dawn and dusk throughout all months of the year (Fig. 4, A–D).

Consistent daily (24-h) and semidaily (12-h) peaks in spectral density were evident from FFTs of depth data for multiple individuals (n=16), indicating strong diel periodicities in vertical movement patterns (Fig. 5A). Longer-term periodicities (0.02–0.14 cpd), on the scale of days to months, were not persistent among individuals (Fig. 5B). Although variability in harmonic frequencies (cpd) was apparent between individuals (n=16), spectral density peaks were perceptible for 9 individuals between 0.044 and 0.048 cpd (21–23 days). Five individuals also showed predominant peaks in spectral density at 0.033 cpd (30 days); however, correlation (coefficient of correlation [r]=0.01–0.19) between depth and lunar luminosity values were low.

There was no significant difference in mean values of VROM between day and night (paired t-test: t=0.49, df=32, P=0.625). However, the mean VROM was significantly greater during the twilight hours (48.9 m h^{-1} [SD 12.3] than during the day (39.6 m h^{-1} [SD 10.8]; paired t-test: t=8.16, df=32, P<0.0001) and nighttime (41.1 m h^{-1} [SD 13.2]; paired t-test: t=5.30, df=32, P<0.0001). Similarly, VROM values exceeded 150 m h^{-1} most frequently around 0500 and 1900 PST (Fig. 6A). In contrast, surface-oriented behavior (depths ≤5 m) reached a minimum during twilight periods, and increased surface activity occurred from 0900 to 1600 PST and from 2300 to 0300 PST (Fig. 6B). Collectively, surface-oriented behavior was heightened from May to September, with a peak in July, but was rarely observed from November to February (Fig. 7).

Horizontal movements

The locations of tag recoveries spanned an 820-km stretch of coastline between La Salina, Baja California Norte (32°01′N, 116°53′W), and Half Moon Bay, California (37°27′N, 122°28′W) (Table 1). The majority of tagged fish (n=22) moved in a northwesterly direction (300–330° heading; mean: 317°) along the California coastline during their time at liberty. Five recaptured individuals moved southeast of their initial tagging location (135–158° heading; mean: 151°), 3 of which were recovered below the border of the United States and Mexico. The reported locations for more than half of the tag recoveries (n=22) were >100 km from the tagging site, and 21% of fish were recaptured between 20 and 100 km from the point of release. After a mean time at liberty of 433 days (range: 9–1154 days), 11 individuals were recovered within 20 km of their initial tagging site. There was no relationship between fish size and net displacement or between time at liberty and net displacement (Table 1).

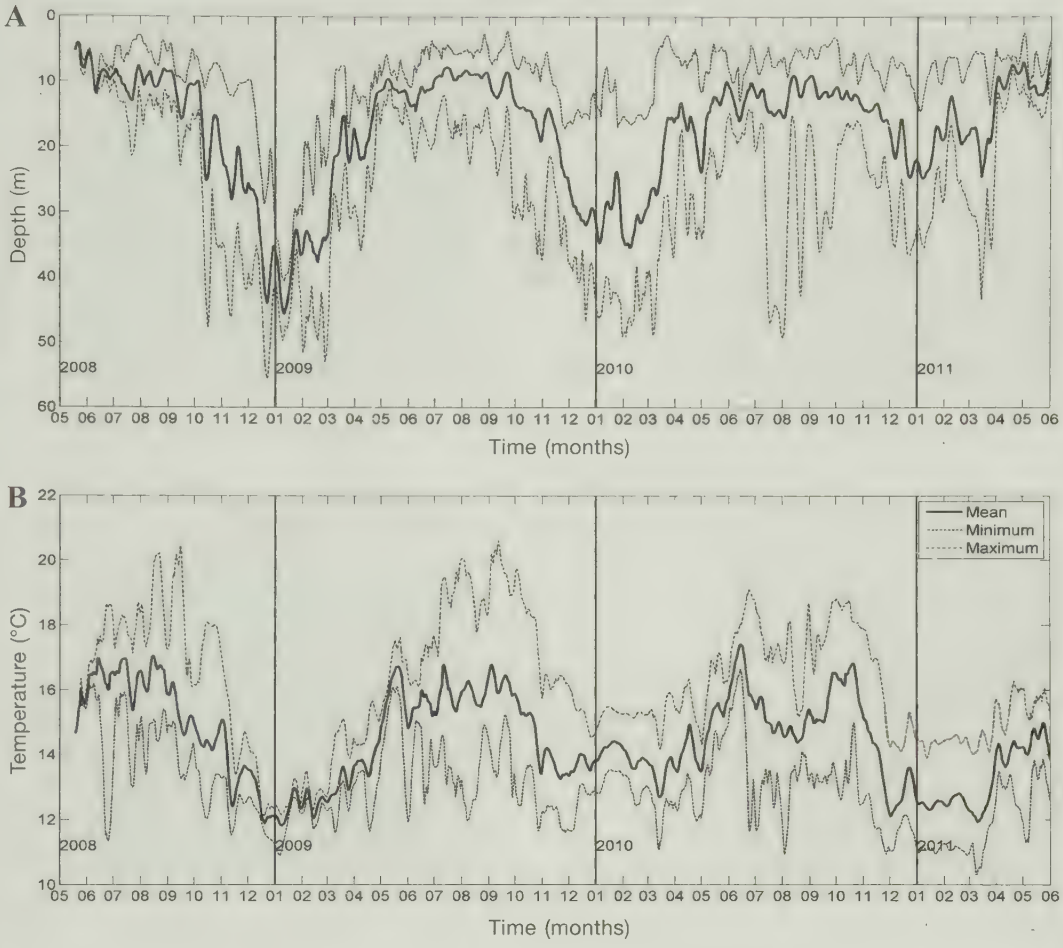

Figure 3

Time-series plots for 16 adult white seabass (*Atractoscion nobilis*) at liberty off California and Baja California, Mexico, between May 2008 and June 2011 (duration ≥12 months), illustrating (**A**) mean daily depth (n=5.21×10^6 observations) and (**B**) mean daily temperature (n=2.61×10^6 observations) values calculated with a 7-day running mean for smoothing.

Temperature profiles

Tagged white seabass experienced water temperatures from 8.8°C to 23.6°C but spent the majority (52%) of time between 13 and 16°C with a peak around 14°C (Fig. 1B). Temperatures ranged between 11°C and 19°C for 95% of all records (Fig. 1B), and 95% of the time that fish spent at depths ≤5 m (i.e., in surface-oriented behavior) occurred at ambient temperatures between 12°C and 19°C. Mean monthly temperatures reached a minimum of 13.0°C in December and a maximum of 16.0°C in June (Fig. 2).

Discussion

This study revealed a relatively high tag recovery rate, providing an extensive data set from fish both temporally and spatially distributed along the California and Baja California coastlines. Despite differences in deployment times and locations, depth and temperature profiles were markedly similar among most fish, and all individuals exhibited seasonal shifts in depth distribution. A significantly shallower and less variable distribution from April to September (than in winter months) contributes to greater vulnerability to most gear types and validates seasonal fishery trends that were suggested nearly a century ago (Skogsberg, 1939). Seasonal and diel shifts in depth distribution, VROM values, and surface-oriented behavior are all indicative of increased feeding and spawning-related activities as water temperatures increase in the spring and summer months. These data provide insight into the migratory nature of the white seabass, along with the first evidence of transboundary movements across the border

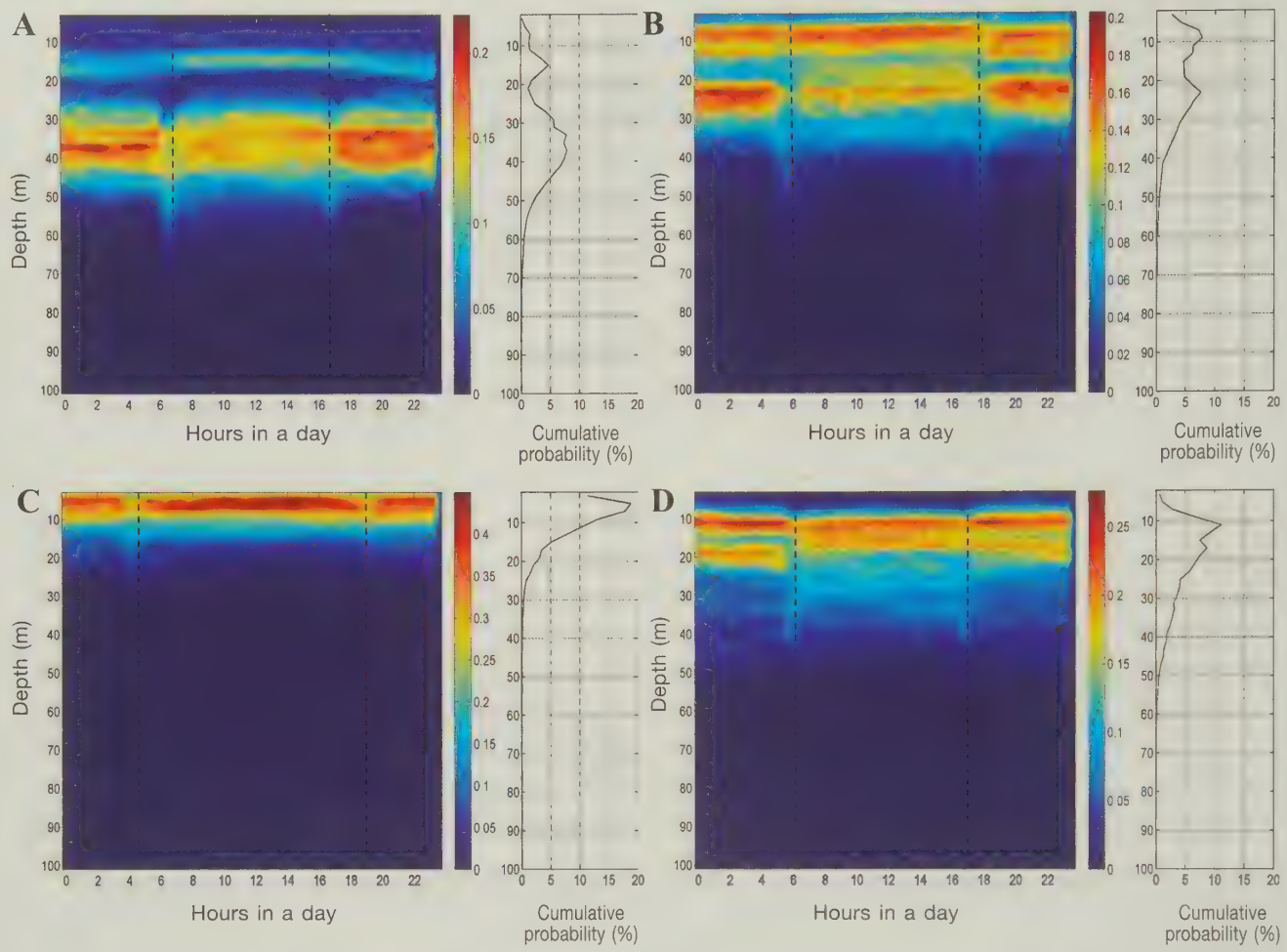

Figure 4

Depth probability plots constructed for the months of (**A**) January (n=267,840), (**B**) March (n=267,840), (**C**) July (n=313,706), and (**D**) November (n=259,200) and summarized over a 24-h period for 16 adult white seabass (*Atractoscion nobilis*) at liberty for ≥12 months along California and Baja California, Mexico, during 2008–2011. Dashed vertical lines represent time of sunrise and sunset to illustrate increased vertical movements around dusk and dawn.

of the United States and Mexico, further supporting the need for a cohesive international management regime for this species.

Tag recoveries

All recaptured white seabass were reported in good physical condition. The dissection of a 125-cm-TL female recaptured 17 days after release revealed that the tagging incision was completely healed and that there was no infection or postrelease trauma. Similarly, in a controlled study to evaluate the effects of surgically implanting V-16 tags (Vemco, Halifax, Nova Scotia, Canada) in wild-caught white seabass (75–124 cm TL), incision sites healed within 90 days, and there were no indications of necrosis or infection (Stutzer, 2004). Stutzer (2004) also found no long-term (450 days) effects on growth, feeding behavior, or survival for the adult white seabass that received tag implants (n=30), versus fish in control (n=20) and sham surgery groups (n=20). Although survival of white seabass was not likely influenced by the capture, handling, or tagging processes, it is possible that other factors (e.g., predation and barotrauma) influenced postrelease survival in the study described here. At least 2 tagged individuals were observed to have been preyed upon by California sea lions (*Zalophus californianus*) directly after release. Increased vulnerability to predation directly after release likely was associated with the effects of exertion, gas bladder inflation, and equilibrium loss experienced during the capture process (Danylchuk et al., 2007).

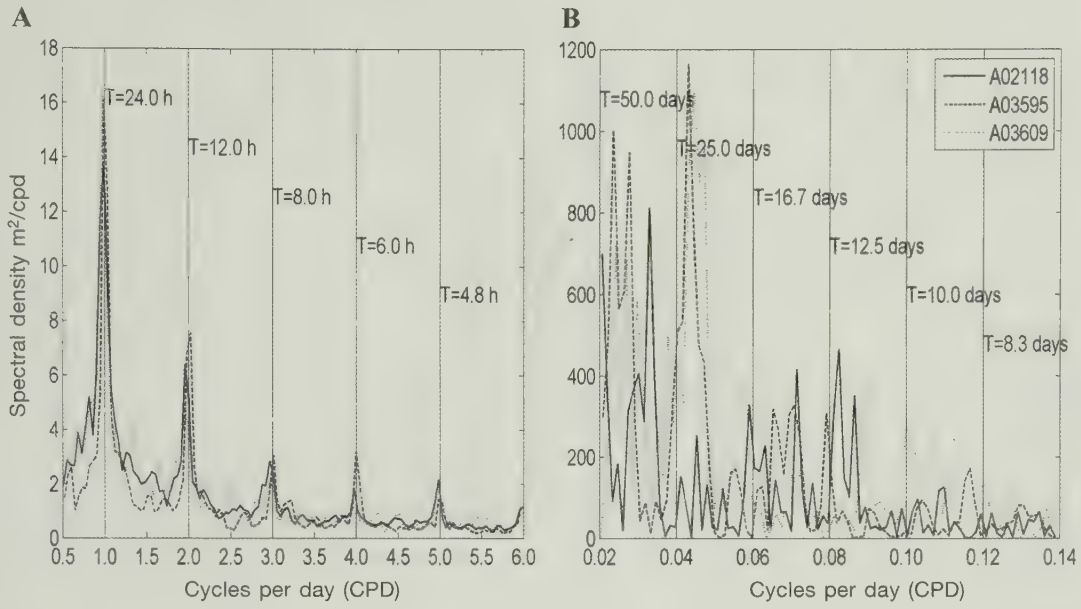

Figure 5

Results of spectral analysis conducted through the application of a fast Fourier transform algorithm to the 3 tracks of white seabass (*Atractoscion nobilis*) with the longest duration (721–740 days; fish A02118, A03595, and A03609) to identify potential depth periodicities on (**A**) diurnal and (**B**) monthly cycles along the coast of California and Baja California, Mexico, during 2008–2011. T=time period.

Other factors that may have resulted in an underestimate of the recapture rate include tag shedding and nonreporting of recaptured individuals. Although a $200 reward was offered for the return of DSTs, it is possible that some recoveries were not reported. Four of the tags recovered in this study were not returned for up to 15 months after the recapture date, further indicating the possibility of under reporting. Therefore, the reported 24% recapture rate is conservative because it does not account for tags that were shed or recaptures that were not reported by the time of the analyses for this study. Given that the average time at liberty was 468 days, the recapture rate may increase further with additional tag recoveries.

The age and size structure of the fish tagged in this study were representative of fish captured in the commercial fishery, as more than 50% of white seabass harvested in California in 2010–2011 were >10 years of age (>112 cm TL) (CDFG[2]). Given that the mean size of white seabass captured in this study was 118 cm TL, all individuals were mature and most tagged fish were >10 years old, and some individuals exceeded 20 years of age (>150 cm TL) (Clark, 1930; Thomas, 1968; Romo-Curiel et al., in press). The ratio of commercial (67%) to recreational (33%) landings in California in 2010 was consistent with the ratio of recaptured white seabass observed in this study, with 68% of tags recovered by commercial fisheries and 32% from recreational anglers (in U.S. waters) (CDFG, 2011).

Of the white seabass tag recaptures, 95% occurred from April to October, a period that directly aligns with seasonal decreases in depth distribution (Fig. 2) and heightened surface-oriented behavior (Fig. 7). Only a single individual was recaptured from December to March, indicating that white seabass are less vulnerable to exploitation upon their dispersal to deeper waters during the winter months. The associations between fish depth distribution and catchability observed in this study are consistent with conclusions on seasonal fishery dynamics from Skogsberg (1939) and others (McCorkle[6]), who have reported that gill nets traditionally were deployed near the surface until mid-October and then set along the bottom from mid-October to December as fish retired to deeper waters. After December, landings were reduced substantially because fishermen were often unable to locate white seabass until the following summer (Skogsberg, 1939). Seasonal recapture trends align with historical fishery data, which indicate that the majority of white seabass landings in California occur from April to September (Skogsberg, 1925; Thomas, 1968). All tag deployments occurred from March to July and peaked in June, a period that directly aligns with the white seabass spawning season (Aalbers, 2008) and validates a heightened vulnerability to capture when fish aggregate to spawn.

[6] McCorkle, M. 2010. Personal commun. Commercial fisherman, Santa Barbara, CA 93109.

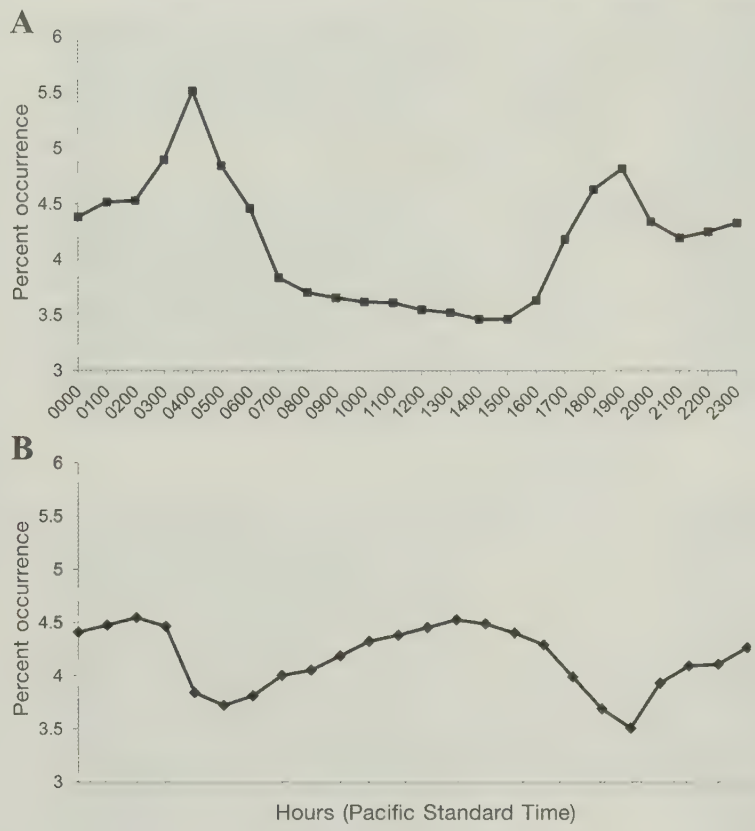

Figure 6

The percent occurrence of all data records from tagged white seabass (*Atractoscion nobilis*) released off the coast of California from 2008 to 2011 showing (**A**) a vertical rate of movement ≥150 m h^{-1} and (**B**) depth values <5 m (surface-oriented behavior), summarized into hourly bins (Pacific Standard Time) and displayed over a 24-h period.

Upon harvest, 77% of recaptured individuals were identified as female, indicating that white seabass sex can be adequately determined on the basis of the detection of sound production during the spawning season. The skewed sex ratio of 3.1:1.0 observed in this study may be related to temporal or size-related segregation among sexes; however, practical inferences cannot be made without a suitable sex-ratio estimate for the wild population.

Vertical movements

The observed shift of white seabass to deeper waters during the winter months may be in response to decreased thermal stratification or possibly to the interrelated effects that these conditions have on prey distribution and availability. As reported for other species, multiple factors, such as changes in oceanographic conditions and prey distribution, contribute to the vertical movements displayed by a species at different times and locations (Hinke et al., 2005; Shepard et al., 2006; Schaefer et al., 2007; Sepulveda et al., 2010). Annual cycles of surface productivity and temperature structure off the coast of California have been shown to influence the vertical distribution of Chinook salmon (*Oncorhynchus tshawytscha*), with deeper profiles documented during the winter months (Hinke et al., 2005). Seasonal shifts in vertical distribution have also been described for Atlantic cod (*Gadus morhua*) (Neat et al., 2006) and yellowtail flounder (*Limanda ferruginea*) (Walsh and Morgan, 2004) in the northwest Atlantic.

Given the interannual variability in the depth and temperature profiles observed for multiple tagged individuals (Fig. 3, A and B), it is likely that seasonal trends in vertical distribution are closely related to localized oceanic conditions. Interannual variation between consecutive winter seasons was evident from the 723-day track of fish A03595, which transitioned from a mean depth of 31.8 m (SD 13.2) in the winter months of 2009–2010 to a mean depth of 8.4 m (SD 3.6) during the winter months of 2010–2011. Similarly, 5 tracks that extended throughout the winter months of 2010–2011 exhibited a considerable reduction in mean depth (18.4 m [SD 7.3]) compared with the 6 tracks recorded in the winter of 2008–2009 (30.8 m [SD 13.0]), but mean temperature values remained consistent (12.8°C) for both sets of time-series data.

Spectral peaks at 1 and 2 cpd may represent increased vertical movements around dawn and dusk, and harmonic peaks at 3 and 4 cpd may indicate weaker movement patterns surrounding daily tidal fluctuations (Fig. 5A). Periodic oscillations in the vertical thermal gradient within the coastal waters off San Diego have been shown to cycle at 6, 8, 12, and 24 h (1, 2, 3, and 4 cpd) relative to internal tidal fluctuations (Cairns, 1968), which typically lag 3 to 5 h behind mixed semidiurnal surface tides (Cairns and LaFond, 1966). Therefore, consistent daily shifts in depth distribution of white seabass may correspond with semidiurnal fluctuations in coastal thermocline depth. Diel and circatidal rhythms in the vertical movement patterns of basking sharks (*Cetorhinus maximus*) also were identified in the northeast Atlantic on the basis of spectral peaks in fine-scale depth records at periods of 1 and 2 cpd (Shepard et al., 2006). In the study described here, inconsistent harmonics in longer period (0.02–0.14 cpd) spectral density plots (Fig. 5B) indicate that the time-series data did not continuously

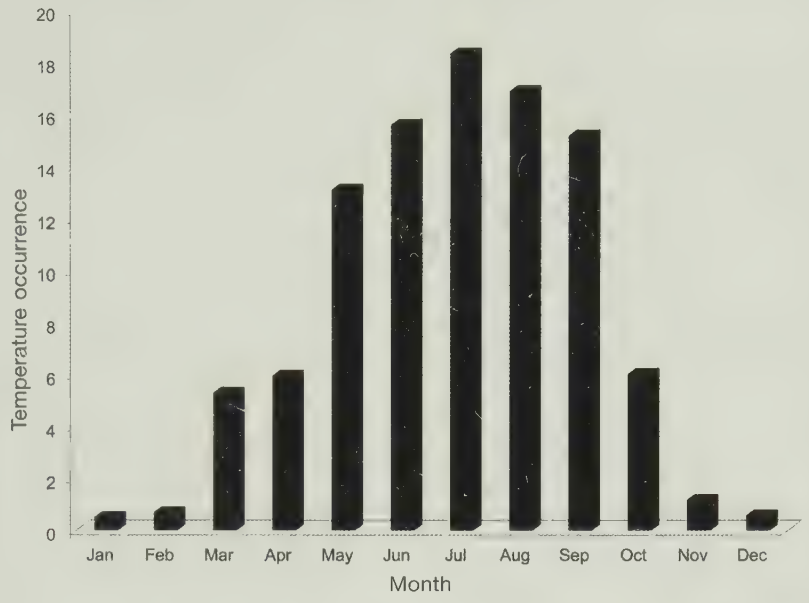

Figure 7

The percent occurrence of all depth values <5 m plotted by month to illustrate periods of surface-oriented behavior for 33 adult white seabass (*Atractoscion nobilis*) tagged and released off California and Baja California, Mexico, from 2008 to 2011.

cycle at regular intervals over prolonged time periods (days to months). If this basic assumption of the FFT algorithm has not been met, then discontinuity would disperse energy throughout all frequencies (cpd), causing considerable noise in the spectral density plots. Additional analyses from tracks of multiple individual fish with extended time-series records may further identify rhythms in vertical movements on a monthly (lunar) or seasonal scale.

Increased VROM values around dusk and dawn indicate heightened crepuscular activity throughout the year. Heightened feeding activity in other fishes and sharks has been associated with crepuscular periods as well as with instances of increased vertical activity (Kitagawa et al., 2004, Sepulveda et al., 2004, Bestley et al., 2008). Higher rates of crepuscular activity indicate that white seabass are effective low-light predators and support fishery information that white seabass are targeted most effectively by hook-and-line fishermen during crepuscular periods (Pfleger[7]). Because the spawning activity of white seabass peaks just after sunset during the spring and summer months (Aalbers, 2008), the increased VROM around dusk may also correspond with vertical excursions associated with spawning-related behavior and broadcast spawning events (Aalbers and Drawbridge, 2008). In contrast, diel surface-oriented behavior was observed most consistently during the midday (0900–1600 PST) and predawn (2300–0300 PST) hours, timing that coincided with periods of reduced vertical activity (Fig. 6, A and B). Surface-oriented behavior has also been described for white seabass during courtship periods within the hours preceding sunset (Aalbers and Drawbridge, 2008), periods when fish may be more vulnerable to spear fishermen and surface gill nets.

Horizontal movements

It was not uncommon for individuals to move more than 500 km from their initial point of release, verifying that white seabass are a highly mobile coastal species. A 109-cm-TL female travelled a net distance of 555 km over a 76-day period from Santa Catalina Island to Monterey Bay, California, at a rate of 8 km day^{-1}. Collectively, a mean displacement of 229 km from the initial tagging location indicates that white seabass are capable of extensive seasonal migrations. Widespread horizontal movements during the spawning season are consistent with recent data that indicate limited residency periods at distinct spawning sites along the southern coast of California (Aalbers and Sepulveda, 2012). The broad movements docu-

[7] Pfleger, T. 2010. Personal commun. Pfleger Institute of Environmental Research, 2110 South Coast Hwy., Oceanside, CA 92054.

mented in our study contrast with the limited home ranges that have been observed in other coastal fishes (Holland et al., 1996; Lowe et al., 2003; Neat et al., 2006). Although 11 of the tagged white seabass were recaptured within close proximity to their release sites after periods of up to 1154 days, interim movements away from the area during their time at liberty may have been substantial. Because fisheries-related information indicates that white seabass tend to reoccur within specific areas from year to year (Thomas, 1968) and considering the mean time at liberty for recaptures with short displacements was near 1 year in our study, it is possible that white seabass maintain an affinity for distinct sites or habitats that are revisited annually for feeding or spawning.

Although the majority of tag deployments occurred around Santa Catalina Island, most tags were recovered within the near-coastal waters. Only 2 tagged fish were recaptured around Santa Catalina Island, and interisland movements were not documented in this study. Seven individuals that were tagged around Santa Catalina Island were subsequently recaptured off the coast of Ventura, indicating a consistent route between Catalina Island and the Ventura flats. An additional 7 fish that were tagged around Santa Catalina Island in May and early June were later caught in the vicinity of Monterey Bay during late July and August of the same or following year, indicating that a portion of the stock traveled up the California coast during the summer months of some years. The high incidence of white seabass tag recaptures in Monterey Bay (26%) corresponds with the recent observed increase in recreational (38%) and commercial landings (22%) north of Point Arguello (CDFG, 2011).

Trends from tag deployments and recaptures indicated that white seabass moved seasonally in a north and westerly direction from July to September, as sea-surface temperatures (SSTs) increased throughout Southern California. Similar movement patterns based on fisheries-related data for Pacific barracuda (*Sphyraena argentea* [see Pinkas, 1966]) and yellowtail jack (*Seriola lalandi* [see Baxter, 1960]) have been suggested for other predatory species of the Southern California Bight. Northward movements of white seabass correspond with latitudinal shifts in SST maxima that follow a seasonal relaxation of coastal wind-driven upwelling and occur later (September–October) to the north of Point Arguello than SST peaks within the eastern Southern California Bight (August) (Legaard and Thomas, 2006; Garcia-Reyes and Largier, 2012). The observed drop in mean temperature values during the months of July–October (Fig. 1B), after a peak in June, may represent decreased SSTs when fish moved above Point Arguello during the summer and fall months, where ambient temperatures are consistently lower than those off the southern coast of California (Reid, 1988). An observed decline in mean depths, temperatures, and VROM values during the late summer and autumn months supports the Skogsberg (1939) hypothesis that white seabass progress northward along thermal fronts as temperatures increase within the Southern California Bight; however, additional data from light-sensitive archival tags with external temperature sensors are necessary to better assess annual migration routes and seasonal trends.

Temperature profiles

Although white seabass occurred across a broad temperature range (8–24°C), data indicate that white seabass occupy a relatively narrow thermal gradient, spending more than half of their time at temperatures between 13° and 16°C (Fig. 1B). Chinook salmon have also been reported to predominantly inhabit a narrow temperature range (8–12°C), indicating that fish may alter their depth in the water column to maintain a persistent thermal experience (Hinke et al., 2005). The relatively consistent temperature profiles from annual time-series records indicate that white seabass may alter spatial and temporal behavior patterns to occupy a particular thermal niche.

Periods of heightened surface-oriented behavior directly aligned with the months in which waters in Southern California exhibit the greatest degree of thermal stratification, with a relatively strong and shallow thermocline present from May to September throughout the region (Cairns and LaFond, 1966). Additionally, a peak in white seabass temperature records (Fig. 1B) corresponds with the 14°C isotherm that is commonly used to identify thermocline depth along the southern coastline of California (Cairns, 1968). However, because tag sensors were implanted within the peritoneal cavity of white seabass, thermal inertia prevented accurate measurement of thermocline depth from tag records. Further, because white seabass occurred over a broad stretch of coastline within areas of high mixing (i.e., upwelling zones and offshore islands) it is difficult to ascertain how thermocline depth influenced vertical distribution in this study.

Future research and management

Heightened fishing effort in conjunction with considerable limitations in essential fishery information warrants the continued need for fishery-independent data sources and active management practices for this species (MacCall et al., 1976; CDFG[1]). Supplementary long-term tagging data, including archived light-level and external temperature records, are currently being collected to provide more specific information on white seabass migration patterns relative to seasonal and interannual variations in oceanic conditions. Additional time-series records from multiple years across the geographic range of white seabass are needed to provide a more comprehensive understanding of fish habitat use, transboundary movements, and temporal shifts in distribution. Furthermore, complementary studies on white seabass stock structure along with a formal

stock assessment with currently available data sources would better enhance our understanding of the population dynamics of this species and facilitate the development of long-term management strategies.

In conclusion, this work provides insight into the seasonal movement patterns, habitat use, and depth distribution of wild-caught white seabass off the coast of California. Distinct seasonal depth distributions were identified with significantly deeper profiles during the winter months. Despite interannual variability, tagged adults spanned a narrow thermal gradient (13–16°C) centered around the 14°C isotherm, indicating the importance of environmental temperature on horizontal and vertical movements. A vertical shift to shallower waters during the spring and summer months directly coincides with the white seabass spawning period and with peak landings and fishing effort. Because of the diverse harvesting methods and seasonally high levels of fishing effort over a broad geographic range, all fisheries must be considered for the effective management and long-term sustainability of this resource.

Acknowledgments

We thank T. Pfleger and family, the George T. Pfleger Foundation, the Catalina Seabass Fund, P. Offield, and the Offield Family Foundation for their generous support. We appreciate donations from the San Diego Fish and Wildlife Commission, the Avalon Tuna Club, Oakpower Unlimited, and the Long Beach Neptunes. We also thank Captain T. Fullam, C. Heberer, M. Okihiro, B. Seiler, V. Wintrode, and K. Lafferty for assistance on various aspects of this work. We appreciate assistance and support from J. Albright and C. Albright, along with cooperation from all fishers that reported tag recovery information. We also thank J. Stopa for aid with graphic illustrations and J. Sepulveda for editorial support, in addition to valuable recommendations by 3 anonymous reviewers. All experiments were performed under valid California Scientific Collection permit 002471.

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Estimating relative abundance and species richness from video surveys of reef fishes

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Abstract—Underwater video sampling has become a common approach to index fish abundance and diversity, but little has been published on determining how much video to read. We used video data collected over a period of 6 years in the Gulf of Mexico to examine how the number of video frames read affects accuracy and precision of fish counts and estimates of species richness. To examine fish counts, we focused on case studies of red snapper (*Lutjanus campechanus*), vermilion snapper (*Rhomboplites aurorubens*), and scamp (*Mycteroperca phenax*). Using a bootstrap framework, we found that fish counts were unbiased when at least 5 of 1201 video frames within a 20-min video were read. The relative patterns of coefficients of variation (CVs) were nearly identical among species and declined as an inverse power function. Initial decreases in CVs were rapid as the number of frames read increased from 1 to 50. However, subsequent declines were modest, decreasing only by ~50% when the number of frames read increased by 300%. Estimated species richness increased asymptotically as the number of frames read increased from 25 to 200 frames, and reading 50 frames documented 86% of the species observed across all 1201 frames. Lastly, we used a generalized additive model to show that the most likely species to be missed were fast-swimming fishes that are solitary or form relatively small schools. Our results indicate that the most efficient use of resources (i.e., maximum information gained at the lowest cost) would be to read ~50 frames from each video.

Manuscript submitted 30 July 2013.
Manuscript accepted 13 November 2014.
Fish. Bull. 113:15–26 (2015).
doi: 10.7755/FB.113.1.2

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

Underwater video sampling has become a ubiquitous approach around the world to index the abundance of marine fish and invertebrate species and to quantify marine biodiversity (see reviews by Somerton and Gledhill, 2005; Murphy and Jenkins, 2010). Although numerous underwater video approaches and techniques have been used to index abundance, many researchers now employ some version of a stationary point-count method with baited remote underwater video stations (BRUVS) (Willis et al., 2000; Cappo et al., 2004). BRUVS sampling has many advantages: 1) it is nonextractive and, therefore, preferred in no-take areas, 2) is less size- or species-selective than other baited gears, 3) can sample deeper waters more easily than diver surveys and do so at lower costs than can autonomous underwater vehicles, 4) provides a permanent record available to be reviewed for accuracy by multiple readers, and 5) can capture habitat characteristics of a survey site and behavioral interactions among species (Silveira et al., 2003; Wells et al., 2008; Langlois et al., 2010; Bacheler et al., 2013).

Nearly all BRUVS studies now use an approach called *MinCount* (or *MaxN* or *MaxNo*) to index the number of individuals of various species present at a site (Ellis and DeMartini, 1995; Murphy and Jenkins, 2010). MinCount is defined as the maximum number of individuals (of each species) present in a single frame during a viewing interval, and this approach is popular because it provides a conservative estimate of the number of individuals of each species present at a site (Ellis and DeMartini, 1995; Willis and Babcock, 2000; Merritt et al, 2011). However, MinCount may be nonlinearly related to actual abundance because it measures a smaller and smaller proportion of individuals present at a site as abundance increases (Conn, 2011; Schobernd et al., 2014). Instead, Conn (2011) proposed an alternative approach, MeanCount, which is calculated as the mean number of individuals observed in a series of frames over a viewing interval. Schobernd et al. (2014) found that MeanCount tracked true abundance linearly with levels of precision similar to that of MinCount. A linear relationship is highly desirable for developing indices of abundance in stock assessment models (Kimura and Somerton, 2006).

A logical next step in the development of the MeanCount approach for indexing fish abundance, as well as in estimating species richness, is to determine the optimal number of frames to be read over a given time interval. Previous studies have shown a strong relationship between

Table 1

Number of video samples (*N*) included in the analyses of reef fishes in the northern Gulf of Mexico, as well as the range of dates, latitudes, and longitudes covered by the samples in 2001–2002 and 2004–2007.

Year	*N*	Date range	Latitude range (°N)	Longitude range (°W)
2001	42	6/14–6/22	27.79–28.35	91.03–93.82
2002	260	2/22–5/30	24.50–30.00	84.26–96.78
2004	169	4/8–6/22	24.59–30.13	82.97–96.30
2005	350	4/20–7/29	24.51–30.13	82.77–96.53
2006	333	4/16–8/4	24.53–30.14	82.77–96.78
2007	389	4/22–8/13	24.50–30.13	82.77–96.77

the time spent surveying and the number of taxa encountered for a wide variety of fish and wildlife species (Fuller and Langslow, 1984; St. John et al., 1990; Barker et al., 1993; Gledhill, 2001), and new methods can account for detection probabilities of <1 when estimating species richness (Nichols et al., 1998; Johnson et al., 2013). Reading more frames will certainly provide more information but will also bring increased costs associated with the additional time and effort required (Rotherham et al., 2007; Al-Chokhachy et al., 2009).

Our objective was to examine the tradeoff between minimizing the effort needed to read videos and maximizing the information obtained. We focused our analyses on 2 primary response variables, each as a function of the number of video frames read. First, we examined potential bias and precision of MeanCount for 3 economically important reef fish species in the Gulf of Mexico. Second, we examined estimates of species richness, defined here as the number of species observed in a video. The results provide general guidance regarding the amount of effort that should be expended to read underwater videos in diverse aquatic systems.

Materials and methods

Data

We analyzed video data from a long-term reef fish monitoring program conducted within U.S. waters of the Gulf of Mexico. These data were collected by the Southeast Fisheries Science Center, National Marine Fisheries Service, in 2001–2002 and 2004–2007. A 4-camera array was deployed with a soak time of 40 min on hard-bottom habitats throughout the sampling range (Table 1) during the reef fish video survey of the Southeast Area Monitoring and Assessment Program. Four Sony DCR-VX2000[1] (Sony Corp., Tokyo) camcorders were mounted orthogonally on a metal array, facing outward, at a height of 30 cm above the bottom (for more details, see Gledhill[2]). Each array was baited with approximately 0.5 kg of squid (*Illex* spp.) in a mesh bag and deployed during daylight hours only. These particular years were selected because they were the most recent years for which data were available before a significant methodological change occurred in video reading procedures.

The reef fish video survey was developed to index reef fish populations and was typically conducted in the spring and summer on shelf-edge reefs from south Texas to the Dry Tortugas in Florida (Fig. 1). A 2-stage sampling design was used to minimize travel time between stations because the survey area was large. For the first stage, we used a stratified random sampling design of randomly selected blocks, each of which was 10′ of latitude by 10′ of longitude in size. Blocks were stratified by 4 geographic regions and by the amount of reef habitat (low or high) present in each block; each block was subdivided into a grid of cells that were 0.19 km by 0.19 km. For the second stage of sampling, cells were randomly selected from within each block. The number of grid cells available for random selection varied depending on how much known reef area was contained in the sampled block.

From each 40-min deployment, 1 of 4 videos was randomly selected, and 20 min of that video was analyzed beginning at the point when video visibility was sufficiently clear for identification of taxa. Fish shape, anatomical features, coloration, and swimming behaviors were used to identify individuals to genus and species levels by using field guides (e.g., Hoese and Moore, 1998; McEachran and Fechhelm, 1998; Carpenter, 2002; Humann and Deloach, 2002; McEachran and Fechhelm, 2005). Video frames were examined every second dur-

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2] Gledhill, C. T., G. W. Ingram Jr., K. R. Rademacher, P. Felts, B. Trigg, and L. Lombardi-Carlson. 2006. SEAMAP reef fish survey of offshore banks: yearly indices of abundance of red grouper (*Epinephelus morio*). SEDAR 12-DW-6, 12 p. [Available from http://www.sefsc.noaa.gov/sedar/download/S12%20DW06%20Video-survey.pdf?id=DOCUMENT, accessed 31 March 2014.]

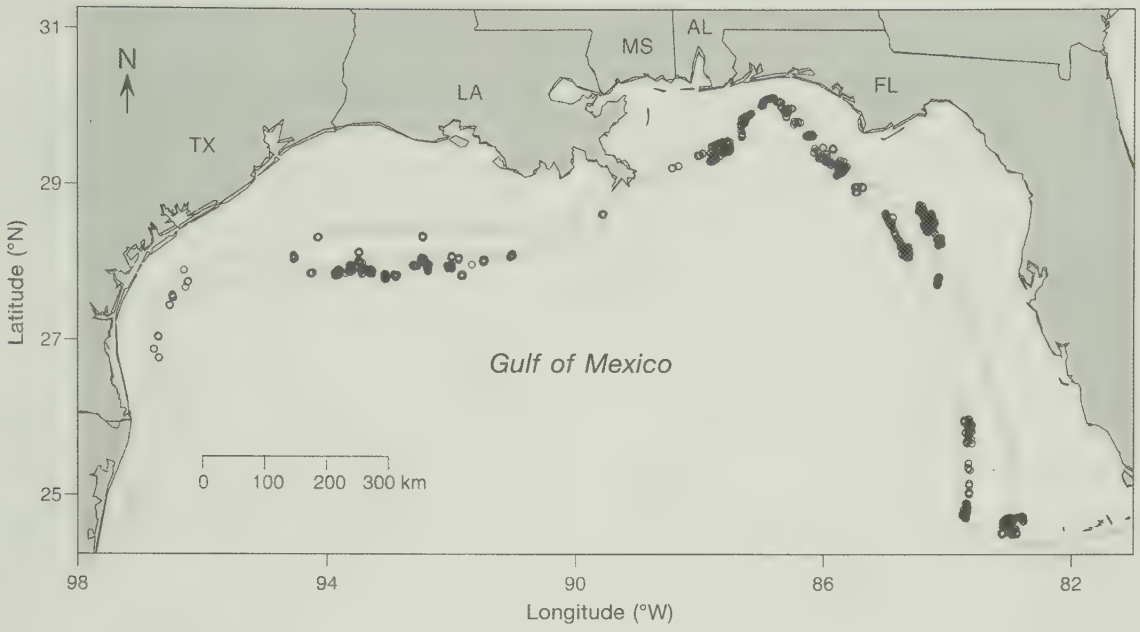

Figure 1

Sampling locations (o) where video was collected during the National Marine Fisheries Service's reef fish video survey in the Gulf of Mexico in 2001–2002 and 2004–2007 as part of its Southeast Area Monitoring and Assessment Program. The light gray bathymetric contour lines indicate depths of 50 and 100 m, respectively. Note that symbols overlap in many cases.

ing the interval from t=0 to t=20 min, resulting in analysis of 1201 frames. Species were recorded if they were listed in the fishery management plans of the Gulf of Mexico or South Atlantic Fishery Management Council or if commercial or recreational landings were known to exist. The resulting list of observed taxa included 210 species (a group, hereafter, called *priority species*). The time each individual fish swam into and out of view (i.e., time in–time out) was recorded for each priority species. Our analysis included only those video samples in which at least one priority species was seen at some point during the 20 min. On the basis of these criteria, 1543 videos were included in our analyses.

MeanCount bias and precision

For a single video v, the MeanCount of a species across video frames was defined with the following equation:

$$MeanCount_{v,F} = \frac{\left(\sum_{f=1}^{F} n_f\right)}{F}, \quad (1)$$

where n_f = the number of individuals observed in frame f; and
F = the total number of frames read.

To examine how MeanCount relates to the number of frames read, we chose as case studies 3 ecologically and commercially important focal species: red snapper (*Lutjanus campechanus*), vermilion snapper (*Rhomboplites aurorubens*), and scamp (*Mycteroperca phenax*). These species were chosen because they vary substantially in terms of body size and schooling behavior. Scamp are generally solitary, red snapper often form small groups, and vermilion snapper often form large groups. Vermilion snapper are also much smaller than red snapper or scamp. Misidentification of these species is very unlikely because of their distinct body shapes and swimming behaviors. Of the 1543 videos examined in our study, red snapper were observed in 375 videos, vermilion snapper in 217, and scamp in 466. MeanCount was computed only from those videos in which the focal species was observed.

For each species, the true MeanCount for each video ($MeanCount_{v,true}$) was computed from the full sampling universe of 1201 frames. That true value was then estimated with a subset of frames with a possible sample size (F) from the interval [1, 200]. The sampling was conducted as follows. First, a list of frames (n=200) was drawn at random and without replacement from the full set of 1201 frames. Then, the first frame of the list (F=1) was used to compute $MeanCount_{v,1}$. Next, the second frame (F=2) was included along with the first to compute $MeanCount_{v,2}$, and so forth until all 200 frames (F=200) were used to compute $MeanCount_{v,200}$.

We quantified bias and precision in estimates of MeanCount with a bootstrap procedure. In the bootstrap, the previously described sampling approach was repeated 1000 times. That is, for each bootstrap iteration b, a new set of 200 frames was drawn to com-

pute MeanCount for every value of F=[1, 2, ..., 200] frames. Therefore, we computed 1000 values for every $\text{MeanCount}_{v,F}$, a choice that expanded our previous nomenclature to $\text{MeanCount}_{b,v,F}$, where b represents a single bootstrap replicate, v represents a particular video sampling event, and F represents the number of frames read.

For each species, we quantified error in estimation using mean relative error (MRE). On the basis of 1000 bootstrap replicates, we computed the MRE for each video in which a species was observed and for each number of frames read with the following equation:

$$MRE_{v,F} = \frac{\sum_{B=1}^{1000}\left(\frac{MeanCount_{b,v,F} - MeanCount_{v,true}}{MeanCount_{v,true}}\right)}{1000}. \quad (2)$$

In addition to their use in determining MRE, we used the bootstrap replicates to compute the coefficient of variation (CV) for each video and for each number of frames read, $\text{CV}_{v,F}$. For graphical presentation, these CVs were scaled to their minima (which occurred at the largest sample size, F=200) to demonstrate the proportional decline in variability in estimates as sample size increased. To quantify the expected response, mean CVs across videos ($\overline{\text{CV}}_F$) were related to the number of frames through the use of a power function, $\overline{CV}_F = aF^b$, where a and b are parameters. These parameters were estimated in log–log space through linear regression, with the following equation:

$$\log(\overline{CV}_F) = a' + b\log(F), \quad (3)$$

where $a' = \log(a)$.

Then, the power function could be inverted to provide the number of frames necessary to achieve a desired mean CV:

$$F = \sqrt[b]{\overline{CV}_F / a}. \quad (4)$$

Species richness

The procedure for estimating species richness for priority species was similar to the one for estimating MeanCount. However, when estimating species richness, we used all 1543 videos. We first computed the true species richness observed in each video ($R_{v,\text{true}}$) as the total number of priority species observed across all 1201 frames. Note that $R_{v,\text{true}}$ is not necessarily the true species richness at a particular site but rather is the species richness observed in an entire 20-min video. That true value was then estimated by tabulating the species richness observed during each increment of the number of frames read, F=[1, 2, ..., 200]. As before, uncertainty in the estimation was quantified with a bootstrap procedure with 1000 replicates, where each replicate (b) contained a set of 200 frames drawn at random and without replacement from the original 1201 frames. Therefore, for each video, we generated 1000 estimates of species richness for each number of frames read, $R_{b,v,F}$.

Once computed, the estimates of species richness were used to evaluate how increasing the number of frames read (F) affected the detection of species known to be present in a video. For this evaluation, we used the average number of species detected across bootstrap replicates, scaled to the true value, with the following equation:

$$P_{v,F} = \frac{\left(\sum_{b=1}^{1000} R_{b,v,F}\right)/1000}{R_{v,true}}. \quad (5)$$

Therefore, $P_{v,F}$ is a proportion equal to zero if no species known to be present were detected on average or equal to one if all possible species were detected on average.

To better understand the estimates of species richness, we related the probability of being observed to behavioral characteristics of those species in videos. Specifically, we considered 2 characteristics of each priority species (s): 1) the mean number of individuals (N_s) seen in a video and 2) the mean duration (D_s; in seconds) each individual was observed in the videos. These mean values for each species were taken across videos in which a particular species was present. To remove rare species for which mean characteristics may be poorly estimated, species were included in this analysis only if observed in at least 10 videos. We then used a generalized additive model (GAM) to relate N_s and D_s, and their interaction, to the proportion of bootstrap replicates (Y_s) in which species s was observed, from all videos where the species was present and where the number of frames read was F=25. We used 25 frames in this study to provide a meaningful contrast across families in the probability of being observed; making such distinctions is important for detecting the effects of predictor variables. All priority species were included in this analysis. Before fitting the GAM, the response variable Y_s was transformed from probability space by using the arcsin squareroot transformation to achieve approximate normality, and predictor variables were taken in log space:

$$\arcsin\left(\sqrt{Y_s}\right) = g_1(\log(N_s)) + g_2(\log(D_s)) + g_3(\log(N_s), (\log(D_s)), \quad (6)$$

where g_1, g_2, and g_3 represent spline functions.

The GAM approach strikes a balance between more simple and more complicated models, and it was chosen for its flexibility and for providing a straightforward interpretation of results. The GAM was implemented in the R programming language, vers. 2.15.1 (R Core Team, 2012) with the mgcv library (Wood, 2006). For presentation, the fitted response was transformed back into probability space by squaring the sine of the response.

Lastly, we summarized the mean duration in a 20-m video segment, mean number of individuals in each vid-

Table 2

Mean duration and standard error of the mean (SE), measured in seconds (s), of individual fishes in video, mean number of individuals in videos, and mean probability that a fish species would be seen in a video segment (for those videos in which that species occurred) summarized by family for only those species seen in at least 10 videos from footage collected during the National Marine Fisheries Service's reef fish video survey conducted in the Gulf of Mexico in 2001–2002 and 2004–2007 as part of its Southeast Area Monitoring and Assessment Program. Mean probability of being seen in a video was calculated for each species as the mean proportion of videos in which a species was observed (on the basis of 25 randomly selected frames) over all videos in which that species was present. Note that the family names for Labridae, Serranidae, and Scaridae follow the Integrated Taxonomic Information System (http://www.itis.gov). Standard errors of the means (SE) are provided in parentheses.

Family	Common name	Number of species	Mean duration (s)	Mean number of individuals	Probability of being seen in video
Opistognathidae	jawfishes	1	504	22	1.00
Priacanthidae	bigeyes	2	921 (SE 127)	3 (SE 1)	0.99 (SE 0.01)
Holocentridae	squirrelfishes	1	132	10	0.96
Pomacanthidae	angelfishes	5	44 (SE7)	16 (SE 9)	0.85 (SE 0.03)
Balistidae	triggerfishes	3	66 (SE 40)	11 (SE 4)	0.84 (SE 0.07)
Pomacentridae	damselfishes	5	35 (SE 6)	23 (SE 7)	0.84 (SE 0.04)
Labridae	wrasses	7	15 (SE 2)	31 (SE 8)	0.80 (SE 0.06)
Serranidae	sea basses and groupers	23	30 (SE 2)	12 (SE 2)	0.78 (SE 0.02)
Chaetodontidae	butterflyfishes	3	31 (SE 3)	11 (SE 2)	0.77 (SE 0.03)
Malacanthidae	tilefishes	2	28 (SE 11)	8 (SE 0)	0.76 (SE 0.05)
Sparidae	porgies	6	14 (SE 2)	22 (SE 10)	0.75 (SE 0.03)
Acanthuridae	surgeonfishes	3	26 (SE 6)	6 (SE 1)	0.73 (SE 0.02)
Haemulidae	grunts	4	25 (SE 8)	22 (SE 6)	0.73 (SE 0.05)
Lutjanidae	snappers	7	12 (SE 1)	37 (SE 9)	0.73 (SE 0.04)
Scaridae	parrotfishes	4	23 (SE 2)	13 (SE 5)	0.71 (SE 0.05)
Tetraodontidae	puffers	2	25 (SE 7)	4 (SE 1)	0.64 (SE 0.13)
Mullidae	goatfishes	2	11 (SE 4)	14 (SE 6)	0.60 (SE 0.00)
Muraenidae	morays	2	40 (SE 4)	4 (SE 2)	0.60 (SE 0.07)
Carangidae	jacks	6	6 (SE 1)	14 (SE 2)	0.40 (SE 0.04)
Sphyraenidae	barracudas	1	18	4	0.34
Scombridae	mackerels	1	5	2	0.17

eo segment, and probability of being observed in each video for each of the families of fishes included in the analysis described previously in this section (Table 2). The purpose of including this table is to inform readers working in tropical and subtropical oceans about those groups of species they are likely to see and those groups that they are likely to miss if adopting a MeanCount approach where a subset of frames is read.

Results

MeanCount bias and precision

The MeanCount estimator behaved similarly for the 3 species that we used as case studies. The central tendency across bootstrap replicates, represented by mean MeanCount, converged rapidly for red snapper, vermilion snapper, and scamp as the number of frames read increased (Fig. 2). MeanCount values for scamp and red snapper were less variable than the results for vermilion snapper (on the basis of 5th and 95th percentiles), and variability for all 3 species decreased when more frames were read (Fig. 2).

Across all sampling events (i.e., all 20-min videos analyzed) in which the focal species was observed, there were no obvious biases in MeanCount for red snapper, vermilion snapper, or scamp at any level of sampling intensity for 25 to 200 frames read (Fig. 3). The variance for each species decreased as the number of frames read increased, a finding consistent with the results of the individually selected video analysis previously described (Fig. 3). Furthermore, the variance surrounding MeanCount was approximately 50% lower for scamp than for either red snapper or vermilion snapper (Fig. 3).

The relative patterns of MeanCount CVs were nearly identical among the 3 species (Fig. 3). As the number of frames increased from 1 to 200, the decrease in CV was initially rapid and then more gradual as more frames were read (Fig. 3). Because of this pattern, the largest reduction in CVs for all 3 species occurred as the number of frames read increased from 1 to 50. When frames read increased from 50 to 200 (i.e.,

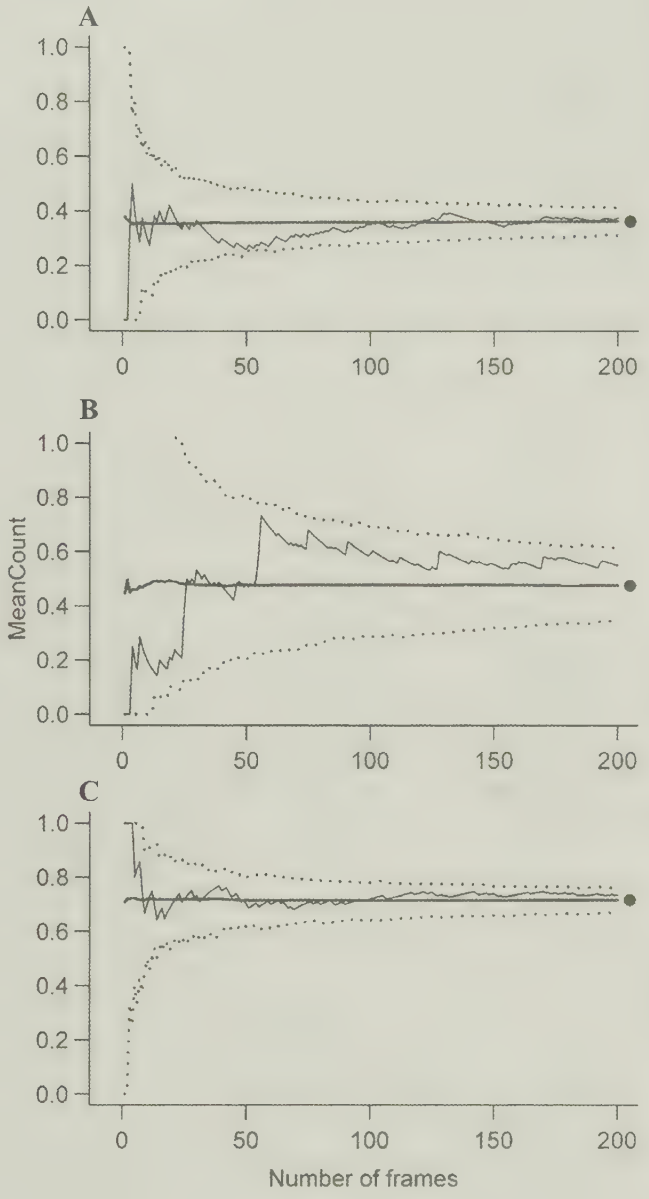

Figure 2

MeanCount, which is calculated as the mean number of individual fish observed in a series of frames over a viewing interval, of a single sampling event (i.e., a 20-min video segment) in the northern Gulf of Mexico as a function of the number of video frames that were read for (**A**) red snapper (*Lutjanus campechanus*), (**B**) vermilion snapper (*Rhomboplites aurorubens*), and (**C**) scamp (*Mycteroperca phenax*). In each panel, the heavy solid line represents the mean of 1000 bootstrap replicates, the lower dotted line represents the 5th percentile, the upper dotted line represents the 95th percentile, the thin solid line is a single bootstrap iteration, and the filled circle on the right is the true MeanCount across all 1201 frames that were analyzed for this study.

300% increase in frames read), CVs only declined by approximately 50% for all 3 species.

In all cases, the relationship between mean CVs and number of frames read was described well by power functions (coefficient of determination [r^2]>0.99; P<0.0001 for F-statistics). Among the 3 species, the estimated relationships show differences in scale (a') but similar rates of decline (b). The mean estimates of parameters and standard errors of the mean (SE) were a'=1.324 (SE 0.004) and b=–0.525 (SE 0.001) for red snapper, a'=1.585 (SE 0.004) and b=–0.524 (SE 0.001) for vermilion snapper, and a'=0.981 (SE 0.004) and b=–0.525 (SE 0.001) for scamp. Because the rates of decline were similar across species, the same number of frames could be read for each if the goal is to achieve a proportional reduction in CV from each species' maximum (which occurred at F=1). However, if the goal is to achieve a particular CV, then each species would require a different number of frames read. For example, a CV of 0.4 would require F=71 for red snapper, F=119 for vermilion snapper, and F=37 for scamp.

Species richness

For illustration, we chose 3 example videos with varying levels of species richness to show general patterns in estimates of species richness. In these example videos, the estimated species richness (number of species observed) increased asymptotically as more frames were read (Fig. 4). Although these 3 videos were chosen simply as examples, they show that the estimates of species richness increased stepwise as the number of frames read was incremented. That is, with the inclusion of each additional frame read, the species count either remained the same if that frame contained no new species or it increased by the number of new species observed. In these examples, the median estimate captured 100% of the species present by around 50 frames for the videos with 3 or 7 species observed but not until around 100 frames for the video that contained 17 species (Fig. 4).

Across all 1543 videos, the proportion of species observed increased with sampling intensity. Most species (median proportion=0.75) were observed in each video when only 25 of the 1201 frames were read, and the median proportion increased when 50 frames (0.86), 100 frames (0.95), or 200 frames (0.99) were read (Fig. 5). On the basis of the interquartile range, however, there was substantial variability among videos, particularly when fewer than 100 frames were read (Fig. 5). When 100 or more frames were read, the variability was lower but some rare species in some videos were still missed.

The GAM explained 87.2% of the deviation in the probability that a species would be observed

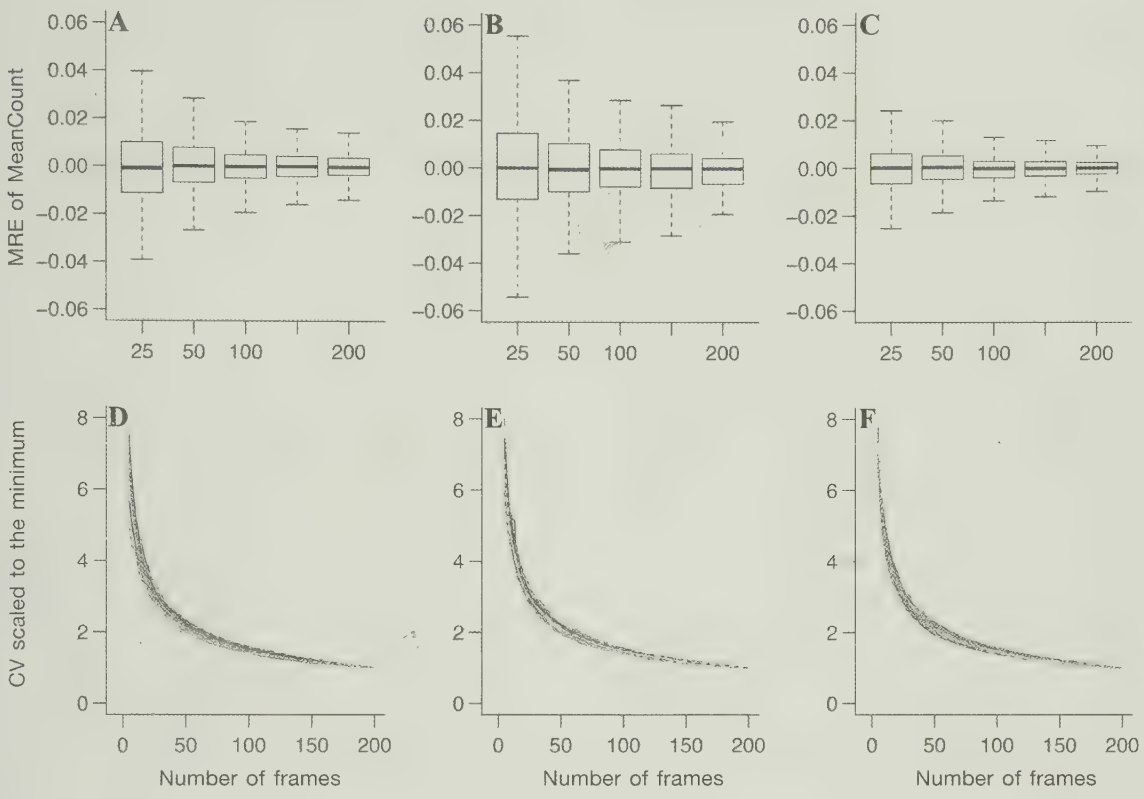

Figure 3

Top row: mean relative error (MRE) of MeanCount, the mean number of individual fish observed in a series of frames over a viewing interval, across all videos analyzed in this study from the northern Gulf of Mexico in 2001–2002 and 2004–2007, as a function of the number of video frames read for (**A**) red snapper (*Lutjanus campechanus*), (**B**) vermilion snapper (*Rhomboplites aurorubens*), and (**C**) scamp (*Mycteroperca phenax*). Boxes represent the interquartile range, thick solid lines represent medians, and whiskers extend to the most extreme data point within 1.5 times the interquartile range from the box. Bottom row: coefficient of variation (CV) of MeanCount as a function of the number of video frames read for (**D**) red snapper (*Lutjanus campechanus*), (**E**) vermilion snapper (*Rhomboplites aurorubens*), and (**F**) scamp (*Mycteroperca phenax*). In each panel, curves represent CVs from each sampling event (i.e., each 20-min video collection), computed from 1000 bootstrap replicates. Each CV curve is scaled to its minimum.

in 25 frames on the basis of the mean duration of each species in a video (estimated degrees of freedom [edf]=1.5; F=36.6; P<0.0001), mean number of individuals in a video (edf=1.0; F=43.9; P<0.0001), or their interaction (edf=7.8; F=0.7; P=0.004). Species were observed with higher probability as their mean time in the videos increased; however, this probability saturated near 1.0 for mean times of 100 s or more (Fig. 6A). Similarly, the probability of being observed increased as the mean number of individuals increased, but, the trend was nearly linear over the range of the predictor (Fig. 6B). The families of fishes that were most likely to be observed in 25 frames of video were the generally sedentary groups like jawfishes, bigeyes, squirrelfishes, angelfishes, and triggerfishes, and those families most likely to be missed were fast-moving groups like tunas and mackerels, barracudas, and jacks (Table 2).

Discussion

In many places around the world, underwater video has become a common approach to monitor the abundance and distribution of marine fish and invertebrate species and to quantify marine biodiversity (e.g., Heagney et al., 2007; Stobart et al., 2007; Brooks et al., 2011; Merritt et al., 2011; Gladstone et al., 2012). For many such studies, BRUVS have been used and have provided an index of the abundance of various species through the use of a stationary point-count with the MinCount method (Ellis and DeMartini, 1995; Willis et al., 2000; Murphy and Jenkins, 2010). Recent research has indicated that MeanCount is more linearly related to true abundance than is MinCount (Conn, 2011; Schobernd et al., 2014). To provide the next logical step in the evaluation of the MeanCount approach,

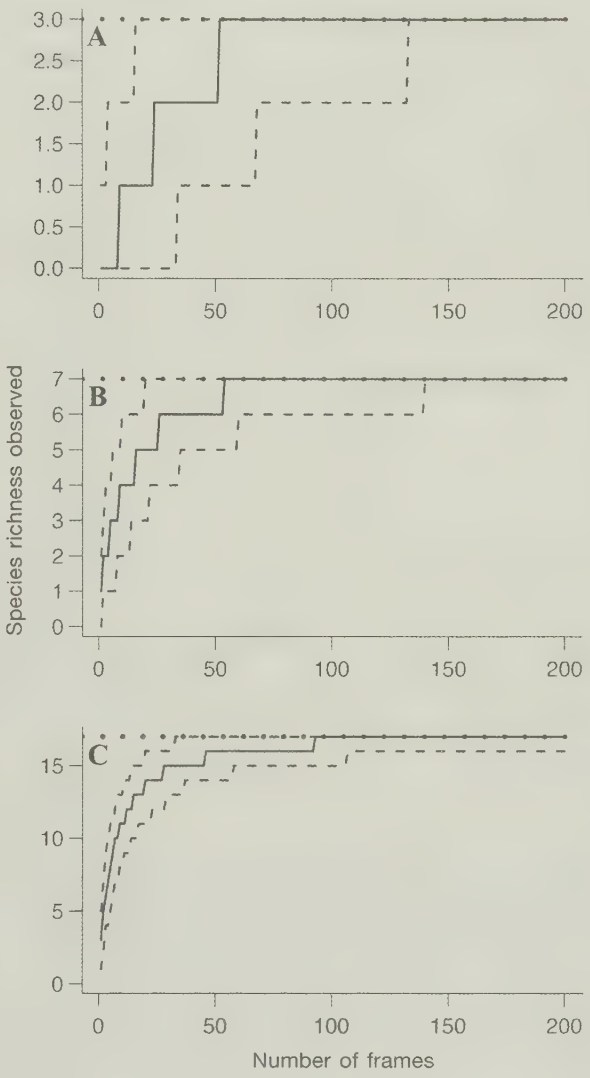

Figure 4

Examples of species richness (total number of species) observed as a function of the number of video frames that were read for this study of the use of video surveys to index abundance and diversity of reef fishes in the northern Gulf of Mexico in 2001–2002 and 2004–2007. Each panel is from a different 20-min video segment that was analyzed and selected to represent a relatively (**A**) low, (**B**) medium, or (**C**) high number of species. In each panel, the solid line is the median value from bootstrap replicates, the lower dashed line is the lower 5th percentile, the upper dashed line is the 95th percentile, and the dotted horizontal line is the total number of species observed in the full video (across all 1201 video frames).

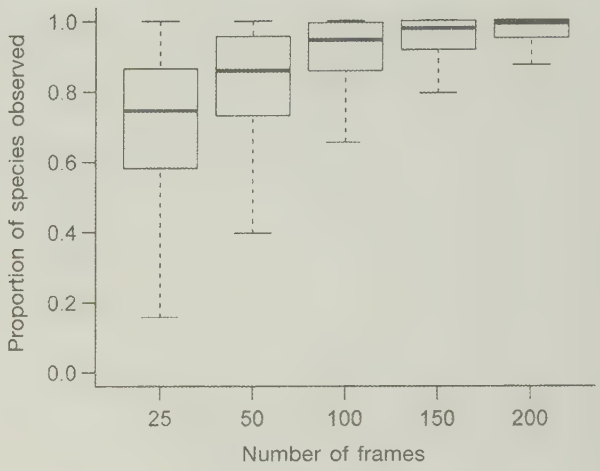

Figure 5

Proportion of species observed across all 20-min videos analyzed in this study as a function of the number of video frames that were read for this study of the use of video surveys to index abundance and diversity of reef fishes in the northern Gulf of Mexico in 2001–02 and 2004–2007. A value from each 20-min video was computed as the mean estimate of species richness (i.e., mean of the number of species observed across 1000 bootstrap replicates) divided by the total number of species known to be present in that video segment (i.e., observed in any of the 1201 video frames). Boxes represent the interquartile range, thick heavy lines represent medians, and whiskers extend to the most extreme data point within 1.5 times the interquartile range from the box.

we examined the tradeoff between time spent reading videos and the information obtained. In this study, we found that reading more frames decreased variability surrounding MeanCount for 3 reef fish species and increased the total number of species observed, but bias was negligible even when a small number of frames were read (e.g., F=25). These results will be useful to researchers in designing and tailoring their underwater video surveys to incorporate MeanCount for estimation of relative abundance or species richness.

Previous studies have shown that the number of taxa encountered in a wide variety of fisheries and wildlife monitoring studies is related to the spatial or temporal extent of sampling (Fuller and Langslow, 1984; St. John et al., 1990; Barker et al., 1993; Gledhill, 2001). We observed an inverse power relationship between CVs and number of frames read and an asymptotic relationship between the number of species observed and the number of frames read. Therefore, CVs decreased and the number of species observed increased dramatically as the number of frames read increased from 1 to 50, but gains in precision were much more modest after that point. These results are similar to results from studies of stream fishes that have documented a threshold of sites sampled beyond which the increase in species observed was negligible (Angermeier and Smogor, 1995; Cao et al., 2001; de Freitas Terra et al., 2013). The number of frames that should

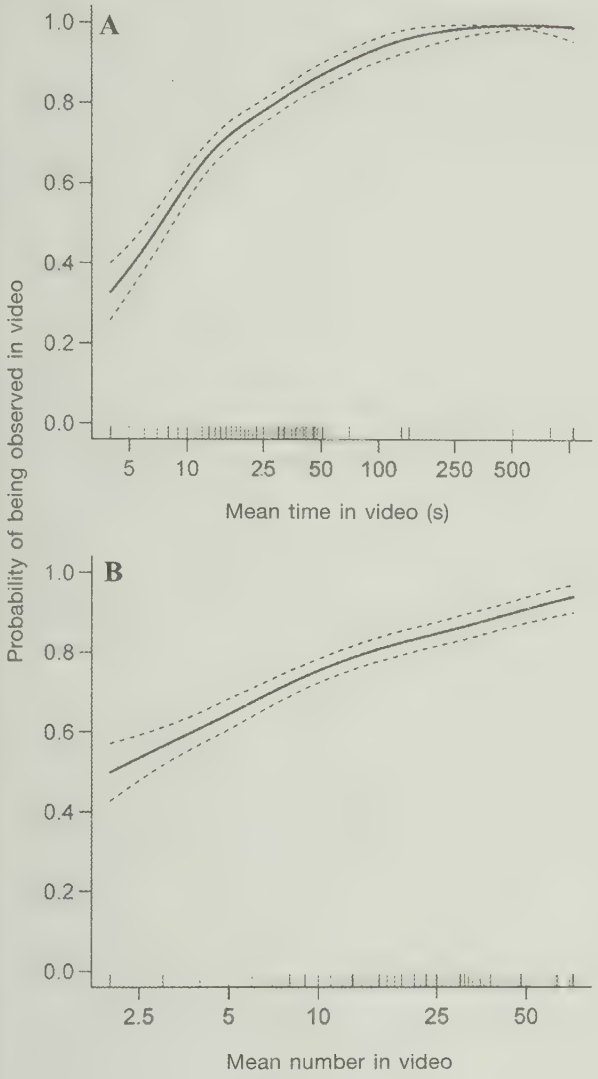

Figure 6

Relationship between the probability of a species being observed in a video segment and (**A**) its mean time in video or (**B**) the mean number of individuals of that species observed in each video. Included in the analysis were 90 reef fish species present in at least 10 videos in the National Marine Fisheries Service's reef fish video survey conducted in the northern Gulf of Mexico in 2001–2002 and 2004–2007 as part of its Southeast Area Monitoring and Assessment Program. The solid black lines indicate fitted relationships from a generalized additive model, the dashed lines are 95% confidence intervals, and the tick marks on the *x*-axis show the distribution of values from the 90 species that were included in this analysis.

be read is likely study-specific and would depend on the total number of videos to be read, the relative importance of rare species, the total resources available for video reading, and time constraints for video reading (Gledhill, 2001). Our results indicate that reading approximately 50 frames from each video may provide a reasonable compromise between costs and information gained, if one can accept that about 14% of species would be missed at each site compared with a reading of all frames in an entire 20-min video segment.

As shown by our GAM results, behavioral characteristics largely determined how likely a species was to be observed or missed in a subset of video frames. Whether a species is observed in a subset of video frames is almost entirely dependent on 2 behavioral characteristics: 1) the mean duration of time spent by each fish in the video viewing area and 2) the mean number of individuals present in each video. Fast-swimming and relatively infrequent fishes, such as tunas, mackerels, barracudas, and jacks, were the ones most likely to be missed and, therefore, tended to be underrepresented in estimates of species richness. These same taxa also had higher absolute CVs around indices of abundance than those for fishes like groupers and snappers that were observed more frequently. We also showed that CVs from observations of a fast-moving, schooling species (vermilion snapper) were more than twice as high as CVs for a slow-moving, nonschooling species (scamp), but the relative pattern of CVs was the same for both species. Clearly, researchers must carefully consider the behavior of their target species when designing a BRUVS sampling strategy with a MeanCount approach, for instance, by allocating significantly more video-reading effort if fast-moving, infrequently encountered species are targeted.

We estimated the proportion of species observed in a subset of frames compared with the number observed in all frames of a 20-min video segment, but note that reading all frames in a 20-min video segment likely underestimates all the species present at a site. For instance, Gledhill (2001) showed that approximately 68% of reef fish taxa in the Gulf of Mexico that were observed in a continuous 60-min video segment were observed in analysis of a 20-min segment. Furthermore, given the exclusively diurnal sampling in our study, nocturnal fishes were likely poorly detected, as were small, cryptic species (Collette et al., 2003; Smith-Vaniz et al., 2006; Williams et al., 2006). Therefore, our results (from an approach for which a subset of frames was read) should be interpreted as a reduction in species observed compared with results from reading of a 20-min video segment, not a comparison with the true species richness at a site.

Researchers could consider approaches that account for the fact that all video reading methods likely miss some reef fish species that are actually present at a site. First, occupancy or *N*-mixture modeling approaches can estimate detection or capture probabilities separately from the underlying distribution or abundance of a species (MacKenzie et al., 2002; Royle, 2004), but multiple site visits may be necessary each year (Issaris et al., 2012) unless spatial autocorrelation is modeled (Johnson et al., 2013). Second, if the emphasis is on es-

timation of species richness over an entire study area, species accumulation (i.e., rarefaction) curves may be a useful approach (e.g., Nichols et al., 1998; Thompson et al., 2003). Species accumulation curves and related approaches (Angermeier and Smogor, 1995) may be especially useful in diverse systems with many rare species (Green and Young, 1993; Gotelli and Colwell, 2001).

Our study design included several simplifications. First, with our bootstrap procedure frames were selected at random for analysis. Alternative approaches may select frames systematically, either with fixed intervals (e.g., one frame every 30 s; Bacheler et al., 2013) or through adaptive sampling. Second, we estimated the proportion of species observed in a subset of frames in relation to all of the species observed in each 20-min video segment. Ideally, our estimates would have been compared with the total number of species occupying the site, but true species richness at each site was unknown (Gotelli and Colwell, 2001). Third, we lacked information on current direction or magnitude; therefore, we were unable to estimate the size or shape of the bait plume, information that can be important in determining the catch or counts of fishes made through the use of baited gears (Collins et al., 2002; Jamieson et al., 2006). Fourth, we did not account for temporal autocorrelation (i.e., samples taken closer in time are likely more similar than those taken further apart; Strachan and Harvey, 1996) when analyzing frames within a particular video. Temporal autocorrelation violates the standard statistical assumption of independence among observations and, when present, may affect the estimated CVs. Temporal correlation is problematic for characterization of diel or seasonal variability but not for quantification of the density or number of species captured in a video. Temporal correlation could be minimized or avoided in practice by not choosing frames clustered in time. Fifth, our study would have been more informative if the costs of reading video frames were known, allowing for explicit cost-benefit analyses related to optimum sample sizes (Cochran, 1977; Thompson, 1992). However, these video data were recorded in a time in–time out format and not by individual frames, and, therefore, the costs of reading each frame could not be estimated.

MeanCount, computed from a sequence of video frames, has been shown to track linearly with true abundance at a site (Conn, 2011; Schobernd et al., 2014)—a critically important issue when standardizing survey data to produce abundance indices for use in stock assessment models (Maunder and Punt, 2004). Our study is the first, however, to document how the number of frames read can relate to CVs around MeanCount for reef fish species and the proportion of reef fish species observed at a site. Previous research has documented the general relationship between the spatial or temporal extent of sampling and CVs or the number of species observed (Fuller and Langslow, 1984; St. John et al., 1990; Barker et al., 1993; Gledhill, 2001). Similarly, we showed that the number of frames read was negatively related to CVs and positively related to the proportion of species observed. More important, however, both relationships were nonlinear and indicate that the information gain slowed substantially after reading approximately 50 frames. Video studies that apply the MeanCount approach to other systems could use our GAM results to help broadly understand how many frames to read, accounting for the behaviors of the species of interest.

Acknowledgments

We thank M. Campbell, C. Gledhill, A. Pollack, and the Pascagoula laboratory of the NOAA Southeast Fisheries Science Center for providing access to the Gulf of Mexico reef fish video data, the staff and crew members who participated in data collection, and the Southeast Area Monitoring and Assessment Program for funding. We also thank M. Campbell, A. Chester, P. Conn, A. Hohn, T. Kellison, P. Marraro, Z. Schobernd, and 3 anonymous reviewers for comments on previous versions of this manuscript.

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Fishery Bulletin
established 1881

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Age, growth, and mortality of gray triggerfish (*Balistes capriscus*) from the southeastern United States

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Abstract—Gray triggerfish (*Balistes capriscus*) sampled from recreational and commercial vessels along the southeastern coast of the United States in 1990–2012 (n=6419) were aged by counting translucent bands on sectioned first dorsal spines. Analysis of type of spine edge (opaque or translucent) revealed that annuli formed during March–June, with a peak in April and May. Gray triggerfish were aged up to 15 years, and the largest fish measured 567 mm in fork length (FL). Weight–length relationships from a different set of sampled fish were $\ln(W)=2.98\times\ln(FL)-17.5$ (n=20,431; coefficient of determination [r^2]=0.86), ln-transform fit; $W=3.1\times10^{-5}\ TL^{2.88}$ (n=7618), direct nonlinear fit; and $FL=30.33+0.79\times TL$ (n=8065; r^2=0.84), where W=whole weight in grams, FL=fork length in millimeters, and TL=total length in millimeters. Mean observed sizes at ages 1, 3, 5, 10, and 15 years were 305, 353, 391, 464, and 467 mm FL, respectively. The von Bertalanffy growth equation for gray triggerfish was $L_t=457\ (1-e^{(-0.33(t+1.58))})$. Natural mortality ($M$) estimated by Hewitt and Hoenig's longevity-based method that integrates all ages was 0.28. Age-specific M values, estimated with the method of Charnov and others, were 0.65, 0.45, 0.38, 0.34, and 0.33 for ages 1, 3, 5, 10, and 15, respectively. Gray triggerfish recruited fully to recreational fisheries by age 4 and to the commercial fishery by age 5. Estimates of total mortality averaged 0.95 across all fisheries for the years 1986–2011.

Manuscript submitted 2 August 2013.
Manuscript accepted 17 November 2014.
Fish. Bull. 113:27–39 (2015).
doi: 10.7755/FB.113.1.3

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The gray triggerfish (*Balistes capriscus*) (family Balistidae) is widely distributed throughout the Atlantic, from Nova Scotia to Argentina and throughout the Gulf of Mexico in the western Atlantic (Briggs, 1958; in Moore, 1967) and, in the eastern Atlantic, from Ireland (Quigley et al., 1993) to southwestern Africa (Longhurst and Pauly, 1987; Kortenang et al., 1996), where tremendous increases in biomass have been observed for this species beginning in the late 1960s (Caveriviere, 1982; Ofori-Danson, 1989). Gray triggerfish exhibit reproductive behavior that is benthic and nest-building (MacKichan and Szedlmayer, 2007; Simmons and Szedlmayer, 2012), and larvae and juveniles have been shown to use drifting mats of brown algae (*Sargassum* spp.) for habitat in the Gulf of Mexico (Wells and Rooker, 2004) and off the Atlantic coast of the United States (Settle, 1993), generally settling out of the pelagic zone to benthic habitats at age 0 and at a mean size of 96 mm in fork length (FL) in the fall (October) (Simmons and Szedlmayer, 2011).

Gray triggerfish are of major importance to the commercial and recreational sectors of the fishery for reef fishes in the southeastern United States (SEUS). Within the recreational sector, estimated annual landings from headboats sampled by the Southeast Region Headboat Survey (SRHS), which is administered by the Beaufort Laboratory of the Southeast Fisheries Science Center (SEFSC), National Marine Fisheries Service (NMFS), averaged 56 metric tons between 1986 and 2011 (Brennan[1]). These landings have equated to an average ranking of sixth among the 73 species managed under the South Atlantic Fishery Management Council's (SAFMC) Snapper-Grouper Fishery Management Plan. Estimated landings from private recreational boats and charter boats, the other component of the recreational sector, averaged 84.5 metric tons annually during 1986–2011 (Sminkey[2]). Commercial fisheries of the SEUS harvested an average of 125.5 met-

[1] Brennan, K. 2013. Unpubl data. Southeast Fisheries Science Center, National Marine Fisheries Service, Beaufort, NC 28516-9722.

[2] Sminkey, T. 2013. Unpubl. data. National Marine Fisheries Service, NOAA, Silver Spring, MD 20910.

ric tons of gray triggerfish annually during 1986–2011 (Gloeckner[3]). Landings are widely distributed along the East Coast of the United States, from North Carolina to southeast Florida. The Florida Keys account for very little in the way of gray triggerfish landings; headboat landings have averaged only 135 kg annually from 1986 to 2011. In terms of rankings of the 2 fishery sectors, the recreational fishery ranks first, averaging 54.6% of the annual catch during 1986–2011, followed by the commercial sector (45.4%).

Gray triggerfish are currently managed by the SAFMC with a minimum size limit of 305 mm (12 in) in total length (TL) in commercial and recreational fisheries off the eastern coast of Florida only and with a daily aggregate bag limit of 20 snappers or groupers per person for recreational fishermen (SAFMC[4]). Commercial harvest of gray triggerfish closes once the annual catch limit has been reached and until the new fishing year begins (for example, this fishery re-opened on 1 January 2014).

Published studies on the aspects of life history of gray triggerfish from the eastern Atlantic include growth (Ofori-Danson, 1989; Aggrey-Fynn, 2009) and reproduction (Ofori-Danson, 1990) studies from Ghana. Studies from the western Atlantic, in addition to the ones previously mentioned, include an age and growth study from Brazilian waters (Bernardes, 2002), 3 unpublished college theses in which the life history characteristics of populations off the SEUS coast or GOM were examined (Escorriola, 1991; Ingram, 2001; Moore, 2001), and a single published age and growth study from the Gulf of Mexico (Johnson and Saloman, 1984).

We studied gray triggerfish from the SEUS because this species is an important resource for all reef fisheries in the SEUS; however, little new biological information has been provided in recent years. Furthermore, updated information on the life history parameters of this fish is needed because NMFS is undertaking the first comprehensive stock assessment of gray triggerfish collected from the Atlantic waters off the SEUS. This study provides information on life history parameters of gray triggerfish collected from the commercial and recreational fisheries of the SEUS and provides a comparison of the new parameter estimates with those from previous life history studies conducted in the SEUS and other areas.

Materials and methods

Age determination

Gray triggerfish were opportunistically sampled from fisheries landings along the SEUS coast from 1990 to 2012 by port agents employed by the SRHS and the SEFSC Trip Interview Program (TIP) to sample commercial fisheries landings. The majority of specimens from both fishery sectors were captured by conventional vertical hook-and-line gear. A small number of fish (n=5) were obtained from fishery-independent sampling that was conducted in Florida with traps used in the black sea bass fishery. Measurements of FL and TL of specimens were recorded in millimeters. Whole weight (W) was recorded for fish landed in the headboat fishery. Fork lengths were measured for all specimens as standard protocol, but not all fish were weighed or measured for TL; therefore, weight–length relationships may have different sample sizes. Fish landed commercially were eviscerated at sea; therefore, whole weights were unavailable. Because of predetermined sampling protocols and time constraints imposed by their workload, samplers were unable to determine the sex of fishery-dependent specimens.

First dorsal spines were removed from 6419 gray triggerfish and stored dry in coin envelopes. Spines were used as aging structures instead of otoliths because gray triggerfish otoliths are small and difficult to extract. Spines were sectioned with a low-speed saw, according to the methods of Potts and Manooch (1995). A single 0.5-mm section was taken from the spine above the condyle. The sections were mounted on microscope slides with thermal cement and covered with mounting medium. Then, the sections were viewed under a dissecting microscope at 12.5× magnification with transmitted light. Each sample was assigned a ring count equal to the number of translucent zones.

Three readers interpreted gray triggerfish spine sections. Two readers (JCP and MLB) each read a separate portion (45%) of the sections, and a third reader (MC) read the other 10%. To ensure consistency among readers in the interpretation of growth structures, each individual read a calibration set of 100 spine sections, and the 2 primary readers each read an additional set of 98 spine sections, for the calculation of an index of average percent error (APE), by following the method of (Campana, 2001).

Increment periodicity was assessed with edge analysis. The edge type of the spine was noted: 1=translucent zone forming on the edge of the spine section; 2=narrow opaque zone on the edge, generally <30% of the width of the previous opaque zone; 3=moderate opaque zone on the edge, generally 30–60% of the width of the previous opaque zone; 4=wide opaque zone on the edge, generally >60% of the width of the previous opaque zone. On the basis of edge frequency analysis, all samples were assigned a chronological, or calendar, age obtained by increasing the translucent zone count by one if the fish was caught before that increment was formed and had an edge with an opaque zone that was moderate to wide (type 3 or 4). All fish caught after translucent zone formation would have a chronological age equivalent to the translucent zone count.

[3] Gloeckner, D. 2013. Unpubl. data. Southeast Fisheries Science Center, National Marine Fisheries Service, Miami, FL 33149.

[4] SAFMC (South Atlantic Fishery Management Council). 2014. Fish ID and regs: gray triggerfish. http://www.safmc.net/fish-id-and-regs/gray-triggerfish, accessed 10 November 2014.

Growth

Von Bertalanffy (1938) growth parameters were estimated from the observed length-at-age data. The chronological age of the fish was adjusted for the time of year caught (Mo_c), therefore, creating a fractional age (Age_f) from the chronological age (Age_c) on the basis of a July 1 birth date (Mo_b):

$$Age_f = Age_c + ((Mo_c - Mo_b)/12). \quad (1)$$

This birth date was selected on the basis of reproductive studies that show that peak spawning of gray triggerfish occurs during June–July in waters off the SEUS (Moore, 2001) and in the GOM (Simmons and Szedlmayer, 2012). Parameters were derived with the PROC NLIN procedure and the Marquardt option in SAS[5] statistical software, vers. 9.3 (SAS Institute, Inc., 1987). A Student's t-test ($P<0.05$) was used to detect if there were significant differences in mean sizes between sectors for the purpose of determining whether pooling of data across sectors was appropriate. We also performed an analysis of covariance (ANCOVA) of length-at-age data by sector (recreational versus commercial), using age as the covariate, to determine whether pooling of data was appropriate (i.e., there were no significant differences in length at age by sector).

Weight–length relationships

We regressed fish whole weight (W, in grams) on fish FL (in millimeters, n=20,431) and TL (in millimeters, n=7618), using data for all gray triggerfish measured by the SRHS from 1972 to 2010 and not just those fish sampled for aging structures. Total length was not measured for many of the fish, and some fish were not weighed. The fish used for age analysis (n=6419) were a subset of the total number of gray triggerfish measured by the SRHS (n=20,431). We regressed FL on TL (n=8065), also with the SRHS data set. For all relationships, we evaluated both a nonlinear fit, using nonlinear least squares estimation in SAS software (SAS Institute, Inc., 1987), and a linearized fit of the log-transformed data, examining the residuals to determine which regression was appropriate.

Total mortality

Age-length keys (Ricker, 1975) were developed for 25-mm intervals by using all aged specimens and the calculation of the age distribution (measured as a percentage) for each interval. Age frequencies for unaged fish by sector were developed with age-length keys (for aged fish) weighted by annual landings from the respective sector and length frequencies (for unaged fish); data for both the landings and length frequencies were acquired from the SRHS, the NMFS Marine Recreational Information Program (MRIP) for samples from recreational fishermen other than those on headboats, and the SEFSC TIP. To optimize the accuracy and precision of our estimates, we ensured that we met the criteria of Coggins et al. (2013) with respect to total sample size (500–1000) and number of aged fish per length bin (at least 10 fish per bin).

Total instantaneous mortality rates (Z) were estimated by using catch curve analysis (Beverton and Holt, 1957). Only fully recruited ages (modal age+1) were used to estimate Z because the age group at the top of the catch curve may not be fully vulnerable to the fishing gear (Everhart et al., 1975).

Natural mortality

We estimated the instantaneous rate of natural mortality (M) using 2 methods.

1) Hewitt and Hoenig's (2005) longevity mortality relationship:

$$M = 4.22/t_{max}, \quad (2)$$

where t_{max} is the maximum age of the fish in the sample;

2) Charnov et al.'s (2013) method, where von Bertalanffy growth parameters are used:

$$M = (L/L_\infty)^{-1.5} \times K, \quad (3)$$

where L_∞ and K are the von Bertalanffy growth equation parameters (asymptotic length and growth coefficient); and

L = fish length at age.

With the Hewitt and Hoenig method, life span or longevity is used to generate a single point estimate, and it is an improvement to the original equation of Hoenig (1983). The newer Charnov method, which incorporates growth parameters, is an improvement to the empirical equation of Gislason et al. (2010) and is based on evidence that indicates that M decreases as a power function of body size. The Charnov method generates age-specific rates of M and is currently in use in Southeast Data Assessment and Review (SEDAR) stock assessments (Williams[6]).

Results

Age determination

A total of 6419 first dorsal spines of gray triggerfish were sectioned. The distribution of samples by area and fishery sector is shown in Table 1. The majority of samples came from the commercial sector in North Caro-

[5] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

[6] Williams, E. 2013. Personal commun. Southeast Fisheries Science Center, National Marine Fisheries Service, Beaufort, NC 28516-9722.

Table 1

Number of samples of first dorsal spines that were available for our age and growth study of gray triggerfish (Balistes capriscus) collected during 1990–2012, primarily from fisheries landings along the coast of the southeastern United States. Five samples were collected during fishery-independent trap sampling off Florida's east coast. Values in the columns for the recreational sector include samples from both the headboat component and the component that includes private recreational boats and charter boats. Samples were collected in the following states: Florida (FL), Georgia (GA), North Carolina (NC), and South Carolina (SC).

	Commercial			Recreational		
Year	FL–GA	NC	SC	FL–GA	NC	SC
1990				18		
1991				5	33	4
1994				1		
1997				2		
2001				2		
2002	8			5		
2003				43		
2004	3	188		60		
2005		386		157	1	
2006		327	140	91	7	13
2007		493	203	17	36	26
2008		676	88	6	13	15
2009		648	92	5	6	21
2010		695	297	1	69	28
2011		1052	220	3	36	23
2012	5					

lina and South Carolina. Approximately 10% of aging samples were from Florida, and the majority of those samples were from the headboat component catches of the recreational sector. Translucent zones were counted on 6267 (97.7%) of the 6419 sectioned spines. Sections from the other 152 spines (2.3%) were determined to be unreadable and were excluded from this study.

For our analysis of increment periodicity, we assigned an edge type to all 6267 samples. Translucent zones were present on the spine marginal edge in all months (Fig. 1); the highest percentage of gray triggerfish with translucent zones occurred from March to June and the lowest from September to February; peak formation occurred in April and May (Fig. 1A). A clear pattern of the width of the opaque margin was noted (Fig. 1B). The narrowest opaque margins (e.g., edge type 2) occurred during June–September, which follows the period of peak formation of the translucent zone. The widest opaque margins occurred during December–March, when the translucent zones start forming again. We concluded that translucent zones on gray triggerfish spines were annuli. Chronological ages resulting from edge analysis were assigned as follows: for fish that were caught from January to June and had an edge type of 3 or 4, the chronological age was the annuli count increased by one; for fish that were caught during the same period and had an edge type of 1 or 2, the chronological age was equivalent to the annuli count; and, for fish that were caught from July to December, the chronological age was equivalent to the annuli count.

Growth increments of gray triggerfish were moderately difficult to interpret. Based on Campana's (2001) acceptable values of APE (5%), agreement was moderate across all 3 readers (MLB–JCP APE=11%, n=198; MLB–MC APE=9%, n=100; JCP–MC APE=12%, n=100; overall APE=11%). Percent agreement values between the 2 primary readers (MLB and JCP) were low (34%) but increased for estimates within (±) 1 year (67%) and within (±) 2 years (86%). An age bias plot indicates that the second primary reader, in comparison with the first primary reader, underestimated gray triggerfish ages, starting at age 5 (Fig. 2), but also shows that the average difference between readers for ages 5–10 was only 1.2 years. These results indicate acceptable between-reader agreement; hence, we included ages from all 3 readers in further analyses.

Growth

Gray triggerfish in this study (n=6267) ranged in size from 173 to 567 mm FL and in age from 0 to 15 years. A single age-0 fish was captured by fishery-indepen-

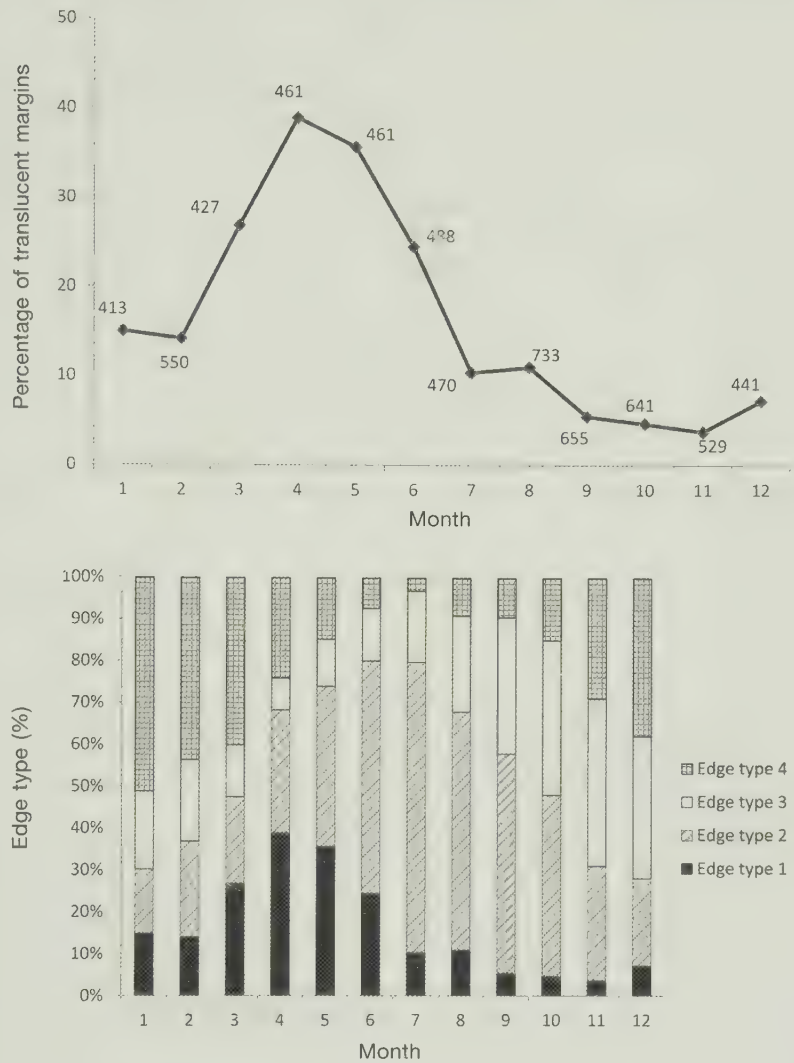

Figure 1

Monthly percentages of (**A**) spine sections with translucent margins on their edges, with monthly sample sizes, and (**B**) monthly percentages of all edge types for gray triggerfish (*Balistes capriscus*) collected from the southeastern United States in 1990–2012. Edge codes: 1=translucent zone on edge, indicating annulus formation; 2=small opaque zone, <30% of previous increment; 3=moderate opaque, 30–60% of previous increment; 4=wide opaque, >60% of previous increment.

dent trap gear, but there were only 13 fish older than age 11 (Table 2). Length and age distributions of the samples by sector (commercial versus recreational) are shown in Figure 3. Visual examination of size and age frequency plots showed no apparent differences in both distributions by sector, with the exceptions that no fish older than age 9 occurred in the recreational samples and commercial samples had fish up to age 15 (Fig. 3A). Modal lengths were 350 mm FL for the commercial sector and 325 mm FL for the recreational sector (Fig. 3B). Mean fork lengths of the specimens by fishery were significantly different: 383 mm FL (standard error [SE] 0.7) for the commercial sector versus 350 mm FL (SE 1.9) for the recreational fishery (t=16.72; df=6253; P=0.0001). The modal age frequency for both fisheries was 4 years (Fig. 3A). Mean ages were found to be significantly different between fisheries: 4.6 years (SE 0.02) versus 4.0 years (SE 0.04) for commercial and recreational sectors, respectively (t=11.9; df=1042.3; P=0.0001).

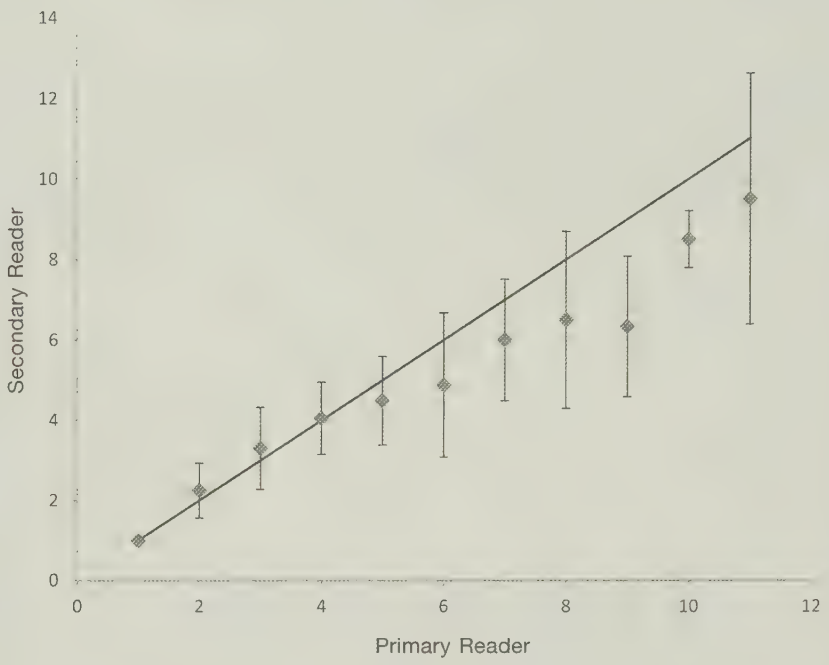

Figure 2

Age bias plot for 198 gray triggerfish (*Balistes capriscus*) sampled from the southeastern United States during 1990–2012 and aged by 2 primary readers. The first reader's mean age estimates are plotted against the second reader's age estimates. Error bars indicate standard deviations.

An ANCOVA of length at age for individual ages revealed no significant differences in size at age between the 2 sectors (P=0.33) for 7 of the 9 ages for which comparisons could be made (Table 3). When the ANCOVA was performed for state, 9 of 11 tests were nonsignificant. On the basis of these results, we pooled data across sectors and states. The resulting von Bertalanffy growth equation was

$$L_t = 457(1-e^{-0.33(t + 1.58)}) \quad (4)$$

for all sectors, states, and sexes combined (n=6267) (Table 4; Fig. 4).

Weight–length relationships

Statistical analyses revealed an additive error term (variance not increasing with size) in the residuals of the W–TL relationship, indicating that a direct nonlinear fit was appropriate. This relationship is described by the following regression:

$$W = 3.1 \times 10^{-5}\ TL^{2.88}\ (n=7618). \quad (5)$$

Residuals of the W–FL relationship exhibited multiplicative error, indicating that a linearized ln-transform fit of the data was appropriate. This relationship is described by the following regression:

$$\ln(W) = 2.98\ \ln(FL) - 17.5,\ (n=20{,}431;\ r^2=0.86) \quad (6)$$

where r^2 is the coefficient of determination. This equation was transformed back to the form

$$W = a \times FL^b \quad (7)$$

after adjustment of the intercept for log-transformation bias with the addition of one-half of the mean square error (MSE) (Beauchamp and Olson, 1973), resulting in this relationship:

$$W = 2.55 \times 10^{-5}\ FL^{2.98}\ (n=20{,}431;\ \text{MSE}=0.035). \quad (8)$$

The relationship between FL and TL is described by the following equation:

$$FL = 30.33 + 0.79 \times TL\ (n=8065;\ r^2=0.84). \quad (9)$$

Natural mortality

Hewitt and Hoenig's (2005) method, which uses maximum age or life span (15 years in this study), estimated that M was 0.28. The method of Charnov et al. (2013), which produces age-specific estimates of M with the use of von Bertalanffy growth parameters, resulted in estimates of 0.65 for age-1 fish, 0.38 for age-5 fish, 0.34 for age-10 fish, and 0.33 for age-15 fish (Table 2).

Table 2

Observed and predicted mean fork length (FL), measured in millimeters, and natural mortality at age (M) data for gray triggerfish (*Balistes capriscus*) collected in 1990–2012 along the coast of the southeastern United States. Standard errors of the means (SE) are provided in parentheses.

Age	n	Mean FL (SE)	FL range	Predicted FL	M
0	1	173	–	181	0.94
1	23	305 (11)	201–394	257	0.65
2	451	333 (2)	214–560	312	0.52
3	1470	353 (1)	190–530	351	0.45
4	1773	375 (1)	229–550	380	0.41
5	1336	391 (1)	221–526	481	0.38
6	684	411 (2)	300–546	417	0.36
7	313	428 (3)	295–543	428	0.36
8	130	444 (4)	330–567	436	0.35
9	53	468 (6)	330–546	442	0.34
10	22	464 (11)	360–550	446	0.34
11	6	416 (30)	323–513	449	0.34
12	4	482 (23)	417–520	451	0.34
13	1	410	–	453	0.33
14	1	496	–	454	0.33
15	1	467	–	455	0.33

Total mortality

Gray triggerfish were fully recruited to the headboat fishery by age 4, to the private recreational fishery by ages 4–5, and to the commercial fishery by age 5. Estimates of Z were similar among all 3 of these sectors. Mean annual estimates of Z for the years 1986–2011 (from all available data) were 0.94 for the headboat fishery and 0.89 for the other recreational fishery. Mean annual total mortality for the commercial fishery was 0.91 for available data (1995–2011, except for 1997 and 2002). Through the use of a pooled catch-at-age matrix across all sectors, Z was estimated at 0.95 (n=15; standard deviation=0.02; range=0.93–0.97). These results equate to an average annual mortality rate of 0.61 across all 3 sectors. Ricker (1975) defined the annual mortality rate A as "the number of fish which die during a year (or season) divided by the initial population number."

Discussion

Gray triggerfish are admittedly difficult to age. First, the use of an external bony structure, the first dorsal spine, to age the fish has some inherent problems, such as possible resorption of the material or damage to the structure—both of which would not likely affect otoliths. Second, the interpretation of the increments on the spines was variable, for reasons such as the spacing between increments and the subjectivity of the presence of false annuli. Because of these problems, we, along with members of the staff of another laboratory that has been involved in aging fishery-independent samples of gray triggerfish, held a workshop to address issues with aging this fish. A robust set of criteria for interpreting the increments on the spine was established during this workshop. Using these newly established criteria, we reread a set of their samples. We found consistent agreement between readers and within readers in our own study, as evidenced by the APE calculations presented in the previous section. Therefore, the results of this study represent the best available information on the longevity and growth of gray triggerfish.

The spine edge analysis conducted in this study strongly indicates that gray triggerfish deposit one annulus per year from March to June and that peak annulus formation occurs in April and May. This result is similar to findings in other studies where peak annulus formation occurred in June and July in gray triggerfish in the Gulf of Mexico (Johnson and Saloman, 1984) and in June in fish from the east coast of the United States (Moore, 2001) (Table 4). The timing of the deposition of a growth increment in Moore's study was concurrent with peak spawning in June and July. Gray triggerfish in the Gulf of Mexico also have exhibited temporally similar times of annulus formation and peak spawning (Simmons and Szedlmayer, 2012).

Weight–length relationships were nearly identical for gray triggerfish from the SEUS and the Gulf of Mexico. The relationship between FL and TL was also similar: FL=30.33+0.79×TL for fish off the Atlantic

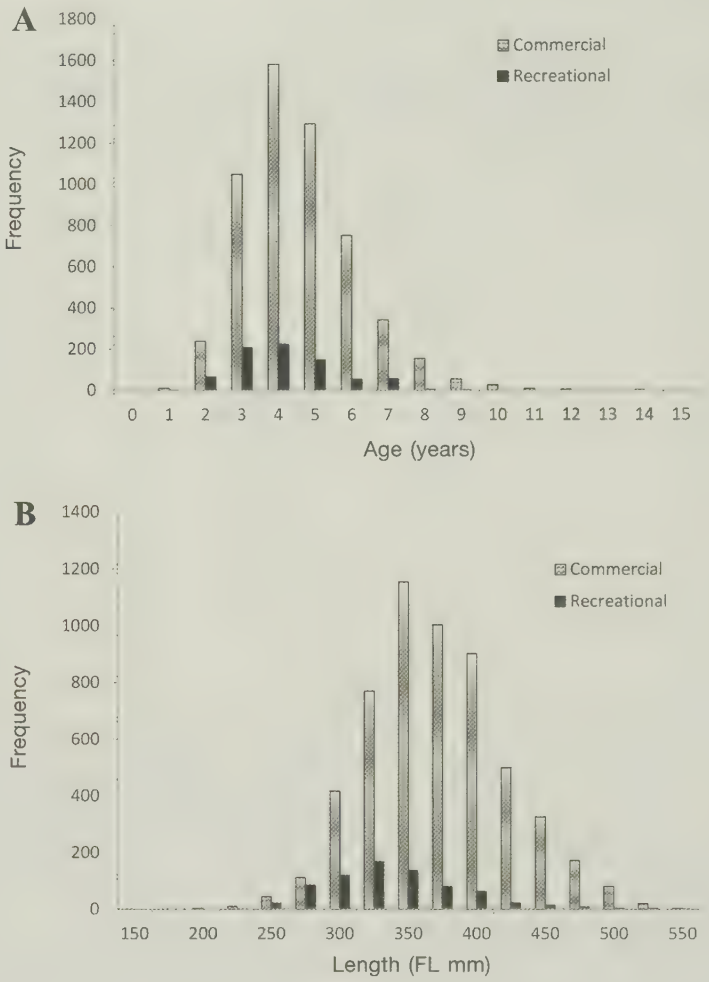

Figure 3

Distributions of (**A**) age frequency and (**B**) length frequency, by fishing sector, for aging samples of gray triggerfish (*Balistes capriscus*) collected from the southeastern United States in 1990–2012.

coast versus $FL=29.70+0.77\times L$ for the Gulf population (Johnson and Saloman, 1984).

Gray triggerfish grew moderately fast, attaining an average observed size of 353 mm FL (14 in) by age 3 (Table 2). This result compares favorably with the finding of Johnson and Saloman (1984) that gray triggerfish from the Gulf of Mexico also grow moderately fast at earlier ages, attaining an average size of 357 mm FL by age 3, growing an average of an additional 50 mm per year through age 5, and averaging gains in growth of 15 mm per year at ages 6–13. Growth of fish in our study slowed after age 3, reaching 496 mm FL by age 5, and then averaging annual size increment increases of 21 mm through age 10.

Several previous studies have found that male gray triggerfish are substantially larger than female fish (Johnson and Saloman, 1984; Moore, 2001; Simmons and Szedlmayer, 2012). These findings justify the generation of sex-specific growth curves if possible. Unfortunately, the specimens we used were collected under sampling protocols that did not allow for the collection of sex-specific data. We recommend that strategies to obtain these data would be beneficial in future studies, if possible.

Because our aging structures came from specimens acquired exclusively from fishery-dependent sources and, therefore, may be more representative of the fished population than the whole population, we advise caution in interpretation of gray triggerfish growth curves, especially for the region of the curve that describes the youngest ages. Minimum size regulations could have an effect on the size of fish available to

Table 3

Results of analysis of covariance of length at age testing for differences by fishery (recreational and commercial) and state (NC, SC, FL–GA) between gray triggerfish (*Balistes capriscus*) aging samples collected during 1990–2012. An asterisk (*) indicates a significant probability value. A dash indicates that the sample distribution did not allow for a test of significance.

Age	*n*	Fishery	State	Fishery*State
0	1	–	–	–
1	23	F=0.03, P=0.87	F=5.76, P=0.02*	–
2	451	F=2.01, P=0.157	F=1.59, P=0.20	F=7.02, P=0.001*
3	1470	F=16.74, P=0.001*	F=0.94, P=0.39	F=1.27, P=0.28
4	1773	F=0.33, P=0.56	F=1.46, P=0.23	F=0.83, P=0.43
5	1333	F=0.23, P=0.63	F=0.81, P=0.44	F=2.76, P=0.06
6	684	F=2.27, P=0.13	F=0.001, P=0.99	F=2.80, P=0.06
7	313	F=4.58, P=0.03*	F=2.06, P=0.12	F=1.09, P=0.33
8	130	F=2093, P=0.09	F=0.63, P=0.53	F=0.03, P=0.43
9	53	F=1.82, P=0.18	F=10.75, P=0.0001*	–
10	22	–	F=0.14, P=0.71	–
11	8	–	F=1.08, P=0.34	–
12	4	–	–	–
13	1	–	–	–
14	2	–	–	–
15	1	–	–	–

generate growth estimates. Even though size limits existed only for fish taken from waters off the eastern coast of Florida during our study (432 of 6267 fish, or 7%), we re-ran the growth model using the method of McGarvey and Fowler (2002), which adjusts for the bias imposed by minimum size limits, and we found no effect of minimum size limits on our parameter estimates. We are confident that our samples represent the smallest fish recruited to the hook-and-line gears. Nevertheless, we collected few fish younger than age 2. It is probable that more comprehensive sampling with fishery-independent gear would capture younger gray triggerfish.

As another strategy to address the lack of smaller, younger fish and the effect this deficiency may have on estimation of the early part of the growth curve,

Table 4

Comparison of life history parameters of gray triggerfish (*Balistes capriscus*) from various studies. L_∞=asymptotic length; K=growth coefficient; t_0=theoretical age at length of zero; SEUS=southeastern United States; and FL=fork length.

	Parameter					
Study	L_∞ (mm)	K	t_0	Peak in translucent edges	Peak spawning	Maximum age (yr)
Johnson and Saloman (1984)—U.S. Gulf of Mexico	466 FL	0.38	– 0.19	June–July	April–May	13
Moore (2001)—SEUS						
Males	521 FL	0.17	–2.03	June	June–July	10
Females	443 FL	0.19	–2.26	June	May–Sept	9
Escorriola (1991)	571 FL	0.19	–0.15	July–Sept	–	13
Burton et al. (current study)	457 FL	0.33	–1.58	April–May	–	15

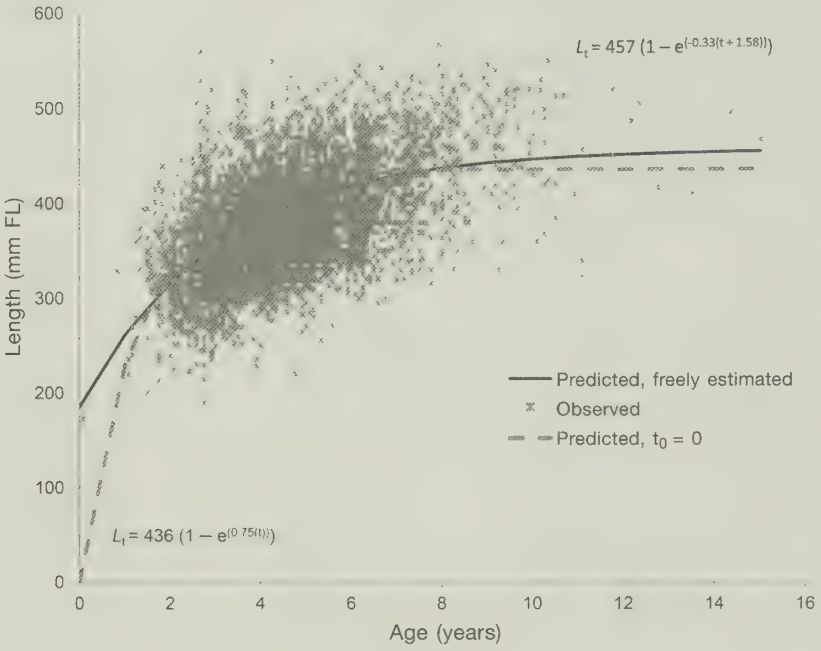

Figure 4

Observed and predicted lengths at age, measured in fork lengths (FLs), for gray triggerfish (*Balistes capriscus*) sampled from the southeastern United States in 1990–2012. L_t=length at age t; t_0=theoretical age when length equals zero.

we recommend estimating growth parameters with a fixed t_0 value, such as −0.5 (Burton et al., 2012) or zero (Burton et al., 2014). This method has the effect of pulling the growth curve down to simulate smaller length at age for fish at the youngest ages. We re-estimated growth parameters of gray triggerfish with a fixed value of t_0=0. The value of the growth coefficient K increased measurably (0.75 versus 0.33, when freely estimated) because of the steepness of the initial part of the curve (Fig. 4). The theoretical maximum length L_∞ decreased marginally, 436 mm FL versus a freely estimated value of 457 mm FL. This result is not unexpected because L_∞ and K are negatively correlated with each other (Ricker, 1975; Xiao, 1994). The 2 growth curves are very similar from age 2 on, with only minor differences in size at age at the oldest ages.

Our theoretical growth curve fitted the observed data well (Fig. 4). Growth parameters estimated in our study compare very closely with the study of gray triggerfish in the Gulf of Mexico (Johnson and Saloman, 1984), and it is interesting to note that fish samples came primarily from fishery-dependent sources in both studies. In Moore's (2001) study, samples were obtained from both fishery-dependent and fishery-independent sources and yielded markedly different growth parameters between male and female gray triggerfish, but no differences in growth parameters estimates were found between the fishery-dependent and fishery-independent data sets.

Natural mortality of wild populations of fishes is difficult to measure. A single estimate of M for the entire life span of a fish is unreasonable, except for fish that have attained a maximal size that renders them invulnerable to large-scale predation. The Hewitt and Hoenig (2005) estimate of M is based on the maximum age a species can attain in an unfished population. In this sense, the point estimate of M, derived with Hewitt and Hoenig's (2005) method, can serve as a lower boundary for the estimate of M derived for older ages by an age-varying method. The maximum observed age from our study was 15—a result that compares favorably with the maximum age of 13 found by Escorriola (1991) and Johnson and Saloman (1984). We feel this age is a realistic maximum age for gray triggerfish because no other study has found an older age, including studies that might be considered more representative of the population at large because they included fishery-independent samples as well (Moore, 2001). We think our estimates are reasonable given that our age-specific estimate of M=0.33 for the older ages that was derived by using the method of Charnov et al. (2013) compares closely with the point estimate of M=0.28 found with the method of Hewitt and Hoenig (2005) (Table 2).

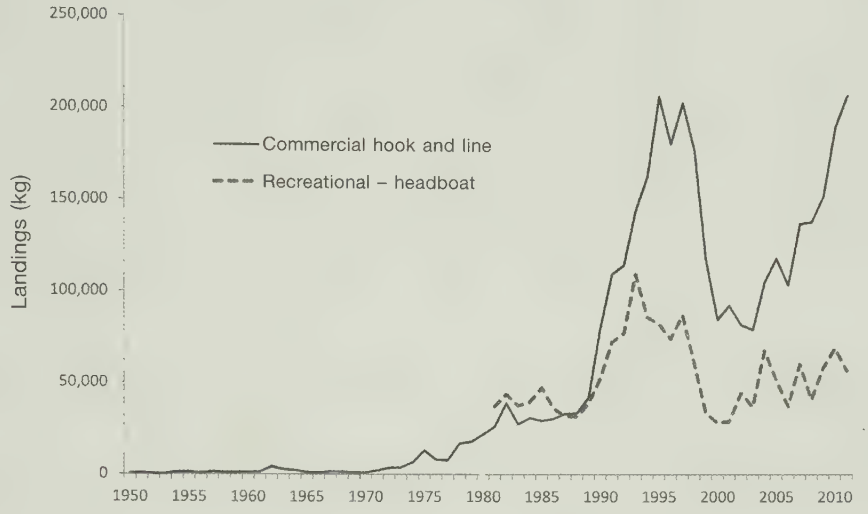

Figure 5

Historical landings of gray triggerfish (*Balistes capriscus*) for the hook and line fishery of the commercial sector and the headboat component of the recreational sector in the southeastern United States in 1950–2012.

Our estimates of Z from catch curve analysis are substantially higher than the values found by Johnson and Saloman (1984) for gray triggerfish in the Gulf of Mexico. The average annual estimate of Z was 0.95 across all sectors pooled, compared with Johnson and Saloman's (1984) estimates of 0.40–0.69, depending on the method used. Whereas they found that recruitment to the hook-and-line gear occurred at age 3, results from our study indicate that full recruitment occurred at age 4 or 5. These observations compare with Moore's (2001) finding of no fishery-dependent samples younger than age 3.

A benchmark stock assessment of gray triggerfish in the SEUS is unavailable, although one is currently underway. A report on trends of static spawning potential ratios estimated for 15 species of reef fishes showed that mean weights for gray triggerfish decreased by an average of 50% in both the recreational and commercial sectors in 1983–99, and catch per unit of effort (CPUE) for the headboat sector increased eightfold during 1989–97 before declining (Potts and Brennan[7]). This drop in CPUE in 1997 coincides with the enactment of the 305-mm minimum size limit in Florida waters; however, we doubt that the regulation caused the drop in CPUE because a small percentage of overall gray triggerfish landings come from waters in Florida.

Both the commercial sector and the headboat fishery of the recreational sector showed marked increases in magnitude of landings around the period from 1989 to 1996 (Fig. 5). Landings leveled off in 2000 for both fisheries but increased again in 2002. We interpret increased landings through the 1990s as an increased desirability by the public for gray triggerfish as a food fish. Before this time, gray triggerfish were mostly discarded by anglers or commercial fishermen because they were perceived as trash fish and unmarketable. Figure 5 shows that the perception of this species as undesirable changed considerably beginning in 1990. Fishermen, especially commercial fishermen, began keeping gray triggerfish when a viable market developed for them. As new regulations limited the harvest of other, more desirable species, fishermen began to target gray triggerfish. The dramatic increase in landings (as well as decreases in mean weight in all fisheries), increases in CPUE in the headboat fishery, and fairly high estimates of total mortality all indicate that gray triggerfish populations in the offshore waters of the SEUS need to be rigorously assessed in terms of stock health and overfishing status.

This study has shown that spine sections in gray triggerfish are reliable structures for aging. The data from this study of gray triggerfish in the SEUS indicate that growth rings are laid down once a year in the spring months and that growth is moderately fast for the first 5 years of life. Estimates of M are reasonable for a fish with moderate life spans (maximum age of 15 years). Estimates of Z are relatively high in the commercial sector and in both components of the rec-

[7] Potts, J. C., and K. Brennan. 2001. Trends in catch data and estimated static SPR values for fifteen species of reef fish landed along the southeastern United States, SEDAR4-DW-28, 41 p. [Available from http://www.sefsc.noaa.gov/sedar/.]

reational sector and are likely a result of the increasing exploitation of this species that is exacerbated by increases in desirability and in marketability to consumers. We believe the results of this study accurately describe the fished population of gray triggerfish in the offshore waters of the SEUS. A NMFS stock assessment is currently underway as of this writing, and we feel the data provided in this study will be a valuable contribution to these efforts.

Acknowledgments

We gratefully acknowledge the many headboat and commercial port agents who provided samples of gray triggerfish over the years. Their efforts made this study possible. J. Smith, T. Kellison, and 3 anonymous reviewers provided valuable reviews that greatly improved this manuscript.

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Economic valuation of stock enhancement of banana prawn (*Fenneropenaeus merguiensis*) in the Strait of Hormuz

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Abstract—Economic return was estimated for the stock enhancement of banana prawns (*Fenneropenaeus merguiensis*) released in waters of the Strait of Hormuz along the coast of Hormozgan Province in Iran. Of the 4.7 million juvenile banana prawns that were cultured and released during the period of June–July 2010, 50,000 were marked by injection with red fluorescent elastomer. During the fishing season in November 2010, 11 marked prawns were recovered (a recovery rate of 0.022%).The mean weight of marked prawns at release and recovery was 1.08 g (± standard deviation [SD] 0.1) and 22.06 g (SD 4.9), respectively, representing a growth rate that ranged from 0.88 to 1.41 g weeks^{-1}. On the basis of the number of prawns released and the recovery rate, the shrimp catch in Hormozgan in 2010 was estimated to be about 1034 released prawns with a mean weight of about 22.80 kg. The production cost for 4.7 million prawns was USD 18,800, and the local market value of landed prawns was USD 3.440 kg^{-1}. Therefore, the total value of the estimated 1034 landed prawns was USD 77.50, indicating a profit to production ratio of 0.0041. These results, particularly the percentage of recaptured prawns, shows that this type of release operation is not economically feasible.

Manuscript submitted 22 June 2013.
Manuscript accepted 12 November 2014.
Fish. Bull. 113:40–46 (2015).
doi: 10.7755/FB.113.1.4

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

The development of the penaeid prawn trawl fishery along the Iranian coast of the Persian Gulf began in 1959 (Van Zalinge, 1984). Shrimp fishing activities by large-scale industrial fleets expanded rapidly, and technology later adapted to artisanal fisheries. Shrimp fishing effort along other Gulf countries soon followed: Saudi Arabia in 1963, Bahrain in 1966, Kuwait in 1967, and Qatar in 1969. Maximum shrimp landings reached 9600 metric tons (t) in Iran for the period of 1964–1965 and 3335 t for Kuwait in 1966–1967, and industrial landings reported by Saudi Arabia and Bahrain peaked at 7400 t in 1973–1974 (Van Zalinge, 1984).

The period of 1959–1969 was a boom phase for the industrial shrimp fisheries that was characterized by high catch rates, increased landings, and the establishment of new companies. In the late 1970s, shrimp catches in the Persian Gulf declined dramatically, and, as a result of that decrease, several fishing companies ceased activities in 1979 (FAO[1]). Increased fishing effort, lower catch rates, and competition with passive types of fishing techniques gradually led to regulatory management measures. These included a reduction in fishing effort, temporal and spatial closures, and, in some cases, total closures of shrimp fisheries. Today, the shrimp fishery in Iranian waters of the Persian Gulf has input and output controls of limited entry, closed seasons, and closed areas. The opening and closure of the fishery (i.e., duration of the fishing season) are flexible. Opening time is based on preseason surveys for estimates of abundance and catch per unit of effort (CPUE) of shrimp, and time of closure is based on the trend of CPUE (kilograms per boat-days) during the fishing season or a final catch rate.

Although more than 16 different species of penaeid prawn are found in the Iranian waters of the Persian Gulf (Niamaimandi, 2006), only 5 species are presently of commercial

[1] FAO. 1981. Report of the third session of the Indian Ocean Fishery Commission for the development and management of the fishery resources of the Gulfs, Doha, Qatar, 28–30 September 1980. FAO Fish. Rep.FAO-FID-R247, 46 p.

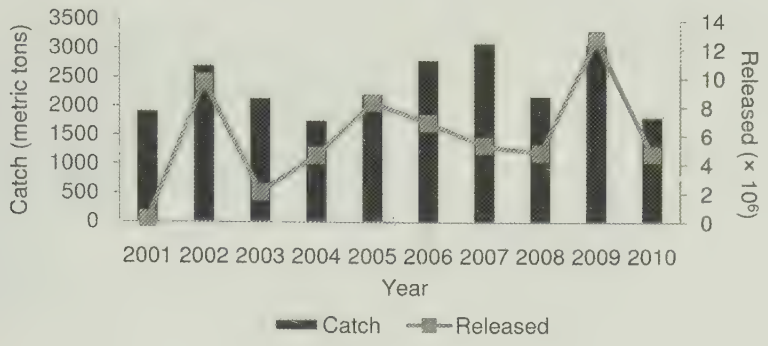

Figure 1

Annual total catches of banana prawn (*Fenneropenaeus merguiensis*), indicated in metric tons by the black bars, and numbers of this species released for stock enhancement (indicated by the line with squares) in waters of the Strait of Hormuz, along the coast of the Persian Gulf in Hormozgan Province, Iran, during 2001–2010.

interest. The banana prawn (*Fenneropenaeus merguiensis*) and Indian prawn (*F. indicus*), both found in the Strait of Hormuz (Hormozgan Province), and the green tiger prawn (*Penaeus semisulcatus*), found in the middle part of Iranian waters (Bushehr area), are the most commercially important shrimp stocks. The Jinga shrimp (*Metapenaeus affinis*) and the kiddi shrimp (*Parapenaeopsis stylifera*), the other important species, are distributed throughout the Iranian waters of the Persian Gulf.

The banana prawn in the Persian Gulf exhibits a fast growth rate and a short life span of around 15–18 months (Zarshenas[2]). The spawning season is very short (February to March) and is followed by a peak in abundance of postlarvae and juveniles present in the shallow coastal mangrove areas from mid-April to July, that then move from these nursery areas to deeper waters at the end of August. The annual catch of banana prawns during the period of 2001–2010 ranged from 1776 t in 2004 to 3122 t in 2009, fluctuating as much as 1000 t between years (Fig. 1).

The decline of prawn fishing in several countries (e.g., Japan, China, Mexico, Australia, and Kuwait) with growing human populations and demands for fishery products led to the development of stock enhancement techniques (Loneragan et al., 2006). The high commercial value of prawns, along with the noted stock decline in the Persian Gulf, generated interest in developing stock enhancement procedures to improve the prawn fisheries. In the Persian Gulf region, Kuwait was the first country that started stock enhancement of shrimp, the green tiger prawn and the kuruma prawn (*Marsupenaeus japonicus*), during 1972–1978 (Farmer, 1981). In Iran, a stock enhancement effort that started in 1995 with the Indian prawn was located in the Persian Gulf along the coast of Hormozgan Province. Wild adult Indian prawns were captured from this area to use for brood stock in aquaculture. However, because of the importance of the banana prawn as a commercial species, stock enhancement of this prawn was started in 2001. During the 15 years of shrimp stock enhancement in Iranian waters of the Persian Gulf during 1995–2010, about 260 million juvenile prawns (mostly Indian prawns, banana prawns, and kuruma prawns) were released at sea.

The annual number of juvenile banana prawn released, as well as the catch of this species between 2001 and 2010, is shown in Figure 1. The mean number of juveniles released was 5.93 billion, and the mean annual catch recorded was 2392 t. Catch of the banana prawn has fluctuated between years during the period of 2001–2010. The lowest and highest levels of banana prawn catch were observed in 2004 (1776 t) and 2007 (3122 t), whereas the minimum and maximum numbers of prawn were released in 2001 (200,000) and 2009 (12.7 billion).

The objectives of this study were to determine the success of the banana prawn stock enhancement program and to evaluate the growth and movement of stocked prawns within the Hormozgan study area.

Materials and methods

The study area was located within the Strait of Hormuz (56°24′E and 27°06′N to 56°26′E and 26°55′N) along estuarine mangrove habitat where depths were <1–3 m (Fig. 2). Wild adult banana prawns were captured from Hormozgan waters and cultured in a pri-

[2] Zarshenas, A. 1991. Shrimp fishery in Hormozgan waters, 27 p. Iranian Fisheries Research Organization, Tehran, Iran. [In Persian.]

vate hatchery center. A florescent elastomeric liquid injection was used to mark 50,000 juvenile banana prawns weighing 1 g each. Injections were made just beneath the skin tissue along a straight path several millimeters long with a 1-cc insulin syringe and a 25-gauge needle (Neal, 1969). Marked prawns were held in fiberglass tanks for 48 hours to observe individuals that may have been injured during marking. Marked prawns were transported by small boats to the sea in fiberglass tanks. The release area was close to the hatchery (about 20 min in travel time by boat). The use of these tanks kept fluctuations in water temperatures from the farm to the release area low, so that the temperatures measured in both areas were similar. Prawns were released through the use of a pumping system.

The mortality rate that resulted from marking and handling of prawn was less than 3%. Dead and moribund prawns were removed before tagged prawns were released to the sea.To prohibit transfer of disease to wild prawn, some specimens of the juvenile cultured shrimps were randomly subsampled to test for the presence of white spot syndrome disease, and prawns were released when no disease was found. Before the release of prawns, the study area was investigated by gill net for shrimp predators; further, releases were made at night to reduce the threat of bird predation. Juvenile prawns were released in mangrove areas, which are nursery grounds of the banana prawn (Staples, 1985; Meager, 2003), in June and July 2010.

Education and outreach efforts to raise public awareness of the release and recapture of prawns for this study included descriptive posters distributed to local persons. In addition, announcements were made in magazines and on national television broadcasts before, and during, the fishing season. A monetary reward program was established that paid the equivalent of USD 10 for the return of each marked prawn. This reward was twice as large as the reward offered in a successful study of tagged and recaptured sailfish (Hoolihan, 2003) that was conducted in the region during 2003–2004.

Costs were estimated for hatchery operation, grow-out, and release on the basis of data from private-sector hatcheries. The hatchery component comprised the brood stock and the hatched larvae. We estimated mean actual costs using the detailed prawn hatchery model, with options for the use of either wild or domesticated brood stock, developed by Preston et al. (1999). The total cost (Ωh) of operations from hatchery production to the point when prawn larvae were 15 days old was calculated with the following equation:

$$\Omega h = \eta Q^{\varphi}, \quad (1)$$

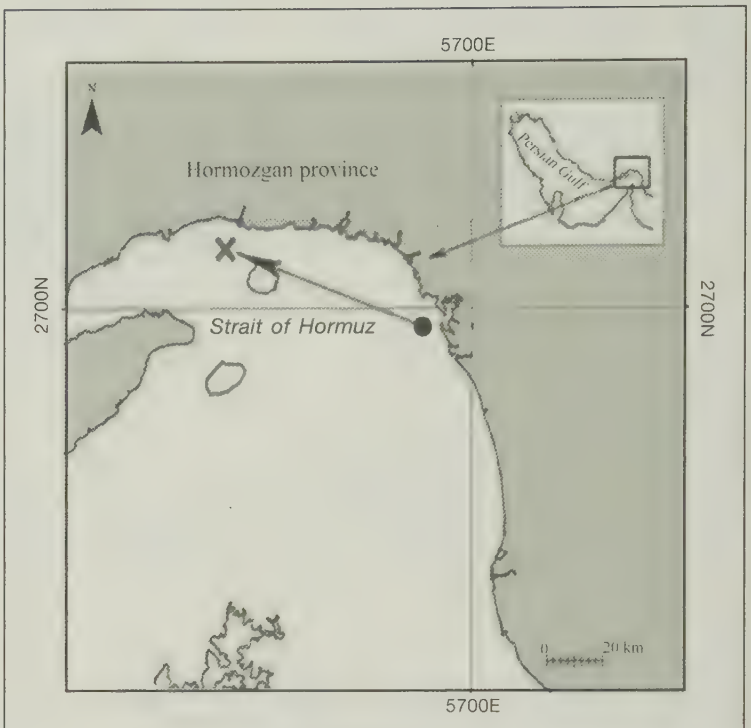

Figure 2

Map of the study area, showing the movement of 11 tagged and released banana prawns (*Fenneropenaeus merguiensis*) in 2010 between the release site (●) and recapture sites (✕) in coastal waters of Hormozgan Province, Iran, in the Strait of Hormuz, the opening that connects the Persian Gulf and the Arabian Sea.

where η = cost per larvae for growth from nauplii to 15-day-old postlarvae (PL15);
Q = the number of larvae produced; and
φ = a parameter describing the economy of scale (i.e., when the scale of production increases, the unit cost of production will decrease). For the present study, φ was calculated at USD 0.0024 per PL15.

The total production (Tp) cost of grow-out of juveniles from PL15 to a weight of 1 g, including prawn feed, employee salaries, and pumping as a part of the operating cost, was calculated using Hannesson's (1993) formula, with some modifications:

$$Tp = (Cp) + (Be - Bi)\gamma\tau, \quad (2)$$

where Cp is the cost of pumping per square meter of raceway in the week, Bi and Be are the initial and end total biomasses of prawns, γ is the cost of feed per kilogram, and τ is the conversion ratio of food to growth in biomass. In the present study, 6.5 million PL15 were produced and 4.7 million juveniles ranging in average weight from 0.98 to 1.2 g were released into the study area. This weight of approximately 1 g was used for released prawns to reduce mortality. For the purpose

Table 1

Weights (g), numbers, and times of release of tagged juvenile banana prawns (*Fenneropenaeus merguiensis*) in estuaries in the Strait of Hormuz along the coast of the Persian Gulf in Hormozgan Province, Iran, during June–July 2010. The standard deviation (SD) of the mean weight is provided in parentheses.

	Mean weight (g)	Number released	Hour of release
	0.98	519,200	22-02
	1.10	494,542	24-02
	1.00	433,000	01-03
	1.40	1,098,332	11-02
	1.00	282,816	11-02
	0.89	733,578	18-02
	1.10	617,269	18-01
	1.20	521,664	20-03
Total	1.08 (0.1)	4,700,401	

of this study, capital investment of the hatchery was not considered. The total cost was the sum of hatchery production cost (Ωh) and juvenile production cost (Tp).

Growth increment (Gw) and growth rate (Gr) were calculated by using King's (2007) formulas:

$$Gw = Gf - Gi \quad (3)$$

$$Gr = w_i / d_t, \quad (4)$$

where Gf and Gi = the average weight of released and recaptured prawns;
w_i = the change in weight between times of release and recapture; and
d_t = the time (in days) between release and recapture.

In the study area, most of the fishing vessels were equipped with electronic geo-positioning systems (GPS), which provided accurate locations of recaptures. GPS information for the release and recapture location was used to estimate days at liberty, movement rate, and distance traveled for recaptured prawns. The distance between release and recapture locations was calculated as a straight line between the 2 locations.

Results

Of the 50,000 prawns that were marked and released overall, 11 (0.022%) were recaptured. The majority of these prawns were reported by local fishermen, and a few were observed by employees in local processing plants.

During this study in 2010, more than 4.7 million banana prawns, each 1 g in weight, were released in the mangrove estuaries in Hormozgan waters. The operation was carried out in June and July. Table 1 shows the numbers of prawns released at different times. The total production cost was approximately USD 0.004 g^{-1} prawn—or 4,700,000×0.004=USD 18,800.

On the basis of the comparison of the number of prawns released (4.7 million) and the recapture rate observed for tagged prawns (0.022%), about 1034 released prawns, with a mean weight of about 22.80 kg, were estimated to have been in the shrimp catch in Hormozgan in 2010.

The average local market price of prawns in 2010 was USD 3.440 kg^{-1}. Therefore, the total market value for the estimated number of released prawns in the catch in Hormozgan was USD 8670. The ratio of catch benefit to expenditures was 77.50:18,800=0.0041.

The juvenile prawns released in shallow waters (at depths of 1–2.5 m) on July 4–11 were recaptured at depths of 20–25 m, after reaching maturity, on Nov. 5–20 (a period of about 18 weeks). Tagged banana prawns moved in northwesterly direction from the release site at 56°56′E, 26°55′N to the recapture site at 56°24′E, 27°06′N in Hormozgan waters—a distance of 46 km (Fig. 2).The estimated rate of linear displacement for recaptured prawns was 310–330 m $days^{-1}$.

The mean age and weight of the 50,000 tagged prawns at release were 8.5 weeks old and 1.08 g (SD 0.1). The mean age and weight of the 11 recaptured prawns were 22 weeks and 22.06 g (SD 4.9). The differences in the weights of prawns between release and recapture were 16–26 g, and the differences in growth rates were 0.87–1.42 g $weeks^{-1}$ (Table 2).

Discussion

In this study, certain factors, such as the choice of release sites, release season, and prawn handling, were carefully controlled to reduce the rate of mortality. In spite of a strong public awareness program, few prawns were recaptured. Success in recognizing individually marked marine organisms in the field requires observer training, mark visibility, and mark retention. Although previous studies indicated that the fluorescent elastomeric tag is a useful method for marking juvenile shrimp and fishes (Neal, 1969; Benton and Lightner, 1972; Frederick, 1997), problems with this method in our study may have contributed to the low recapture rate. For example, growth of tissue adjacent to the elastomeric mark reduced visibility of the mark in the recaptured prawns. Another contributing factor may have been a lack of prior training of observers that would have allowed them to identify marks.

In a study in China, other tagging methods (e.g., hanging tag brands, unilaterally extirpating eyestalks, and cutting uropods) were used and resulted in estimated recapture rates for juvenile fleshy prawns (*Fenneropenaeus chinensis*) from 0.001% to 1.510%. Such low recapture percentages likely were affected by tag shedding, death of tagged individuals by mechanical injury, and regeneration of the uropod (Wang

Table 2

A comparison of the growth of 11 banana prawns (*Fenneropenaeus merguiensis*) that were released and recaptured in waters of the Strait of Hormuz, along the coast of the Persian Gulf in Hormozgan Province, Iran, in 2010. *Gw*=growth increment, or change in weight (g) from release to recapture; *Gr*=growth rate (g weeks^{-1}); CL=carapace length (mm); and *W*=weight (g).

Released shrimp		Recaptured shrimp			
CL (mm)	*W* (g)	CL (mm)	*W* (g)	*Gw* (g)	*Gr* (g weeks^{-1})
13.95	1.2	28.57	17.4	16.2	0.88
13.95	1.2	28.63	17.5	16.3	0.88
12.90	1.2	28.63	17.5	16.3	0.88
12.95	1.2	28.63	17.5	16.3	0.88
13.95	1.2	29.57	17.5	16.3	0.88
13.00	1.1	29.57	19.1	18.0	1.02
12.50	1.0	33.69	27.2	26.1	1.41
11.55	1.0	33.69	27.2	26.3	1.42
13.90	1.1	33.69	27.2	16.1	0.87
13.95	1.1	33.74	27.3	16.2	0.88
13.80	1.1	33.74	27.3	16.2	0.88

et al., 2006). The similarly low recapture percentages observed in our study may also have been affected by the first 2 of those factors.

The low number of recaptured prawns identified in our study makes extrapolation of contribution of released prawns to the total catch tentative. The calculated contribution derived from the 11 recaptured prawns that were reported must be considered a minimum estimate because other tagged prawns may have been recaptured but not recognized or reported. However, the extremely low number of recaptured prawns that was reported gives no evidence that the contribution of released prawns to the total catch was profitable at the study area in 2010.

In this study in Hormozgan waters, banana prawn juveniles moved from shallow mangrove estuaries to deeper waters. The movement of juvenile banana prawns from mangrove habitat to offshore waters has been described already in different regions (Rothlisberg et al., 1985; Staples and Vance, 1985; Vance et al., 1996). Although the rate of recapture of marked prawns, at 0.022%, is too small to allow for making well-supported inferences, our findings show that the seasonal movement of the banana prawn is from inshore to offshore areas. The results of this study indicate that the banana prawn is not highly migratory and that recaptured prawn were caught mostly within 46 km of their release location, despite a period of liberty of 126 days.

Frusher (1985) reported that banana prawns in the northern Gulf of Papua (Papua New Guinea) exhibited maximum movements of 167 km for males and 190 km for females. The majority of all recaptured banana prawns exhibited rates of movement of less than 500 m days^{-1}. A comparison of the movement of banana prawn in our study in Iranian waters and in the Frusher (1985) study in Papua New Guinea indicates that this species migrates over greater distances during its entire life cycle than it does in the limited time of our study and that the number of recaptured shrimp might have been greater if the fishing season had been longer.

The main goal of the stock enhancement program for management of the prawn fishery in Iran was to increase the biomass of banana prawns. Management goals in most fisheries require accurate catch data, abundance estimates, measures of genetic diversity, and estimates of enhancement costs, as well as on a fisherman's willingness to pay and on the monitoring of conflicts (Lorenzen et al., 2010). Release of cultured juveniles would not be effective if there is insufficient nursery habitat to support them (Loneragan et al., 2004; Hamasaki and Kitada, 2006). In our study, the percentage of recaptured prawns did not support the economic feasibility of this type of release operation. An increase in total prawn catch due to the release of shrimp was estimated to account for about 2.5 t, a low proportion (<1%) of total catch. The difference between costs and revenue indicates that the stock enhancement program was not profitable, with a ratio of catch benefit to expenditures of 0.0041. This ratio would undoubtedly be reduced further if capital expenditures were considered.

The economic findings from stock enhancement reported from other areas indicate varying degrees of success. A shrimp stock enhancement program for

the giant tiger prawn (*Penaeus monodon*) in a periodically enclosed lagoon of Sri Lanka was reported to be economically feasible and successful in increasing catches (Davenport et al., 1999). Despite a long history of prawn stock enhancement in Japan and China, economic reports on efforts there do not indicate a profitable experience in all instances. For example, only 5 out of 40 attempts at stock enhancement of the kuruma prawn in Japan proved economically profitable (Loneragan et al., 2006). In evaluations of the bioeconomics of stock enhancement programs for the fleshy prawn in China, cost-benefit ratios of 1:5.2, 1:7.8, and 1:8.5 were reported (Xu et al., 1997; Wang et al., 2006). However, it was not clear what costs were included in these calculations or whether these cost-benefit ratios provided accurate estimates of the real economic returns from stock enhancement (Loneragan et al., 2006).

The results of our study on the stock enhancement of the banana prawn in the Persian Gulf are limited. Further studies are essential to clarify the economical feasibility and biological justification of shrimp stock enhancement programs in this area. Marking in multiple locations with multiple colors and different sizes may provide a better evaluation of stock enhancement operations. Additional studies are needed to assess potential release sites at nursery grounds in this area, to determine optimum size at release, and to improve tagging methods. Hatchery practices may also introduce deleterious effects on the genetic makeup of released stock and, therefore, threaten the wild population. Such effects may range from mild, or undetectable, to severe (Ward, 2006). For future studies in the Persian Gulf area, it would be beneficial to determine and monitor the genetic structure of both wild prawn populations and populations held in captivity before release and throughout the study period. Experimental studies of the effects of other factors, such as the size of prawn at release (different sizes could be released), time of year of release, and the fitness of released prawns before release, also would give information that could increase the probability of success.

Although attempts at prawn stock enhancement in the Persian Gulf by the Iran Fisheries Organization occurred over the 15-year period of 1995–2010, the results of this activity have not been previously documented. The study described here investigated the economic return of the stock enhancement effort for one year only, 2010.

In general, the model used in this study estimated that it would require about 200,000 juveniles, each about 1 g in weight, to produce 1 t of additional catch for the total catch of wild banana prawns. Therefore, 200 million juveniles would be needed to produce an additional catch of 100 t. Some of production costs, such as capital investment, are not fully known and were not included in the model used in this study. These expenses would increase the estimates of the cost of production. On the basis of the market price for banana prawn (USD 3.440 kg^{-1}), the costs of juvenile production (USD 0.004 g^{-1} prawn), and our analysis of 2010 data, it is clear that stock enhancement of this species in Iran is not profitable.

Acknowledgments

This study was funded by the United Nations Compensation Commission and Iranian Fisheries Research Institute. The authors wish to thank K. Aeenjamshid for their assistance with equipment and field work and M. Momeni, M. Darvishi, K. Khajehnoori, I. Ghaeeni, and the staffs of the Persian Gulf and Oman Sea Ecological Research Institute, Hormozgan branch of the Iran Fisheries Organization, and Pars Abzistan Co. for participation in the tagging program and use of their facility.

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Comparison of 4 aging structures in the American shad (*Alosa sapidissima*)

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Abstract—Multiple structures can be used for the age determination of fishes. Choosing the structure that provides the most precise ages is important for the provision of consistent data for the management of commercially and recreationally important species, such as the American shad (*Alosa sapidissima*). In this study, we compared the precision of age estimates obtained from sagittal otoliths, vertebrae, scales, and opercula as structures for the age determination of American shad. Two readers examined structures removed from 462 American shad, which were collected from the Merrimack River in Lawrence, Massachusetts, during May and June of 2008–2010. The precision of age estimates were evaluated by comparisons of ages from different readers and structures. Age estimates determined from otoliths were the most precise (76.2% agreement, 2.99% coefficient of variation). Ages derived from scales were overestimated in young (≤5 years) fish and underestimated in older (≥7 years) fish, compared with ages determined from otoliths. Age estimates determined from vertebrae agreed with those obtained from otoliths better than ages from any other structure tested, but they were less precise and vertebrae required more processing than otoliths. Opercula were difficult to read, resulting in underestimation of the ages of fish that were age 5 and older. The results of this study indicate that the sagittal otolith is the most appropriate structure for determining the age of American shad.

Manuscript submitted 25 October 2013.
Manuscript accepted 25 November 2014.
Fish. Bull. 113:47–54 (2015).
doi: 10.7755/FB.113.1.5

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

The American shad (*Alosa sapidissima*) is an anadromous fish found from the Gulf of St. Lawrence in Canada to the St. Johns River in Florida (Walburg and Nichols, 1967; Hassleman et al., 2013). It is the largest species of the family Clupeidae found in waters of the United States (Walburg and Nichols, 1967), and individuals commonly reach sizes of 50 cm in total length (TL) (Scott and Leim, 1966; Scott and Scott, 1988; Collette and Klein-MacPhee, 2002). This species spends most of its life in saltwater but returns to freshwater rivers and streams in the spring to spawn. Most individuals return to spawn for the first time at age 4 or 5 (Walburg and Nichols, 1967; Scott and Leim, 1966; Leggett and Carscadden, 1978; Ross, 1991).

The American shad is a culturally and ecologically important species. This shad is a sought after game fish by recreational anglers, who prize it for its roe. It also composes an important forage base for many species of fishes (Ross, 1991). Populations of American shad have declined because of fishing pressure and dams that have caused a loss of access to their spawning grounds (Ross, 1991; Latour et al., 2012; Raabe and Hightower, 2014). These factors all make management of American shad important.

American shad are commonly aged by Cating's (1953) scale technique, in which counts of transverse grooves are used to identify the most probable locations of annuli. Recent studies have discredited the accuracy of this method (McBride et al., 2005; Duffy et al., 2011, 2012; Upton et al., 2012). Recently, the use of otoliths to age American shad has been evaluated and validated as accurate with fish of known age for ages 3–9 (Duffy et al., 2012). However, Beamish and McFarlane (1983) have recommended validation of an aging technique for all reported ages and an exploration of alternative aging structures.

The choice of aging structure is critical because not all structures are suitable for age determination of a given species. For example, although scales were historically used to age the white sucker (*Catostomus commersonii*), Beamish and Harvey (1969), after verifying yearly deposition of annuli, found that pectoral-fin rays yielded older ages than did scales of individuals older than age 5. Later studies on white suckers found that fin rays yielded biased ages in the oldest individuals and that the otolith was the most appropriate structure (Thompson and Beckman, 1995; Sylvester and Berry, 2006). These examples show the importance of evaluating each structure for age determination.

For many species, the otolith is the preferred structure. Otoliths were found to be more suitable for aging than were scales for a large number of species, such as lake whitefish (*Coregonus clupeaformis* [Barnes and Power, 1984]), striped bass (*Morone saxatilis* [Welch et al., 1993; Secor et al., 1995]), white crappie (*Pomoxis annularis* [Boxrucker, 1986]), bluefish (*Pomatomus saltatrix* [Robillard et al., 2009]), bull trout (*Salvelinus confluentus* [Zymonas and McMahon, 2009]), Dolly Varden (*Salvelinus malma* [Stolarski and Sutton, 2013]), and summer flounder (*Paralichthys dentatus* [Sipe and Chittenden, 2001]). Although comparisons between scales and otoliths have been relatively common, more comprehensive studies that involve multiple structures are rarer. Scales, otoliths, vertebrae, opercula, and subopercula were used to age pontic shad (*Alosa pontica*) in two recent studies that included the family Clupeidae [Yilmaz and Polat, 2002; Višnjić-Jeftić et al., 2009]), yet no such comprehensive study has been completed for the American shad.

The Interstate Fishery Management Plan for Shad and River Herring requires that biological data, including ages, be collected for American shad annually by states from Maine to Florida (ASMFC[1]). These data are used to make informed decisions regarding the management of this species (ASMFC[2]). Specifically, age data are used to estimate mortality, determine the age of recruitment into spawning populations, and characterize the age structure of populations by sex. Current data used for these purposes are based on scales, which have been shown to produce unreliable ages (McBride et al., 2005; Duffy et al., 2011, 2012; Upton et al., 2012). Given the importance of age data for the assessment and management of American shad, it is imperative that an unbiased and precise aging method be used. The objective of this study was to compare the precision of age estimates obtained from the scales, otoliths, opercula, and vertebrae of American shad.

Materials and methods

American shad were collected by dip net from the fish lift at the Essex dam in Lawrence, Massachusetts, on the Merrimack River during May and June of 2008–2010. American shad were distinguished from other species by morphological characteristics described by Collette and Klein-MacPhee (2002). Samples were frozen and transported to the Annisquam River Marine Fisheries station in Gloucester, Massachusetts. After thawing overnight, TL in millimeters, weight in grams, and sex were recorded for each fish. Sagittal otoliths, scales, opercula, and vertebrae were removed and stored for processing.

Otoliths were rinsed in water and stored dry in microcentrifuge vials. Whole otoliths were placed in a black dish filled with mineral oil and viewed with reflected light through a dissecting microscope at 30–40× magnification for age determination. Left and right otoliths were examined side by side to aid in discerning between annuli and checks. The distal surface of the otoliths provided the clearest view of the annuli.

Scales were stored dry in envelopes before being cleaned in an ultrasonic bath with a 5% pancreatin solution (Whaley, 1991). From 3 to 5 clean, nonregenerated scales were dried with a paper towel and placed between 2 glass slides. Scales were viewed with transmitted light at 5–10 × on a digital computer imaging system that included Image-Pro Plus[3] image analysis software, vers. 6.2 (Media Cybernetics, Inc., Rockville, MD). All scales on a slide were examined to discern annuli from checks, but the scale with clearest annuli was used for age determination.

Opercula were stored frozen before they were boiled for 2–3 min. A small brush was used to clean excess flesh from opercula after they were boiled. The opercula were then rinsed in clean water and air dried for at least 24 hours. Dry opercula were held up to a fluorescent light source, and annuli were enumerated without magnification. Opercula were viewed as pairs to help discern between annuli and checks.

Vertebrae numbers 4–10 were separated with a scalpel. Excess flesh was removed with a scalpel before the vertebrae were soaked for 24–48 hours in a solution of 3% hydrogen peroxide. After the soaking of the vertebrae, a small brush was used to remove any remaining flesh, and the vertebrae were allowed to air dry for at least 24 hours. Whole vertebrae were viewed under reflected light at 20–30× with a digital computer imaging system with Image-Pro Plus software. All vertebrae from each fish were examined to discern between annuli and checks. The vertebra with clearest annuli was selected for age determination.

Annuli in the otoliths, opercula, and vertebrae were defined as the distal edge of each hyaline zone. We used Cating's (1953) definition of annuli on scales, although we did so with disregard for their position in relation to the location of the transverse grooves because the number of transverse grooves within each annulus as outlined by Cating (1953) was discredited by Duffy et al. (2011). Because all fish in this study

[1] ASMFC (Atlantic States Marine Fisheries Commission). 1999. Amendment 1 to the Interstate Fishery Management Plan for Shad & River Herring. Fishery Management Report No. 35 of the Atlantic States Marine Fisheries Commission, 77 p. [Available from http://www.asmfc.org/uploads/file/shadam1.pdf.]

[2] ASMFC (Atlantic States Marine Fisheries Commission). 2012. River Herring Benchmark Stock Assessment, vol. 1. Stock Assessment Report No. 12-02 of the Atlantic States Marine Fisheries Commission, 392 p. [Available from http://www.asmfc.org/uploads/file/riverHerringBenchmarkStockAssessmentVolumeIR_May2012.pdf.]

[3] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

were captured during the time of presumed annulus formation, the edge of each structure was counted as the final annulus.

Only fish for which all 4 structures were deemed readable were included in this study. Each structure was read independently by 2 readers with no knowledge of fish size, sex, or ages assigned to other structures. Readers used scales, otoliths, opercula, and vertebrae from fish not included in the study to familiarize themselves thoroughly with each type of structure before beginning the final reading. Precision of readings was measured with percent agreement and coefficient of variation (CV) (Chang, 1982) 1) between results for one reader and results for the other reader for each structure, 2) among results for reader 2 for a randomly assigned subsample of 100 fish, and 3) between results for otoliths and results for each of the other 3 structures for each reader. Coefficients of variations were calculated with the equation as shown in Campana (2001):

$$CV_j = 100\% \times \frac{\sqrt{\sum_{i=1}^{R} \frac{\left(X_{ij} - X_j\right)^2}{R-1}}}{X_j}.$$

This equation gives the CV for the j^{th} fish,
where X_{ij} = the ith age estimate of the j^{th} fish;
X_j = the average age estimate of the j^{th} fish; and
R = the number of times that fish was aged.

Coefficients of variations listed in this article were averaged across all fish aged. Wilcoxon rank sum tests were used to determine whether differences in age readings existed between otoliths and the other structures. Significance was not tested for fish of ages 3 and 11 because of insufficient sample sizes.

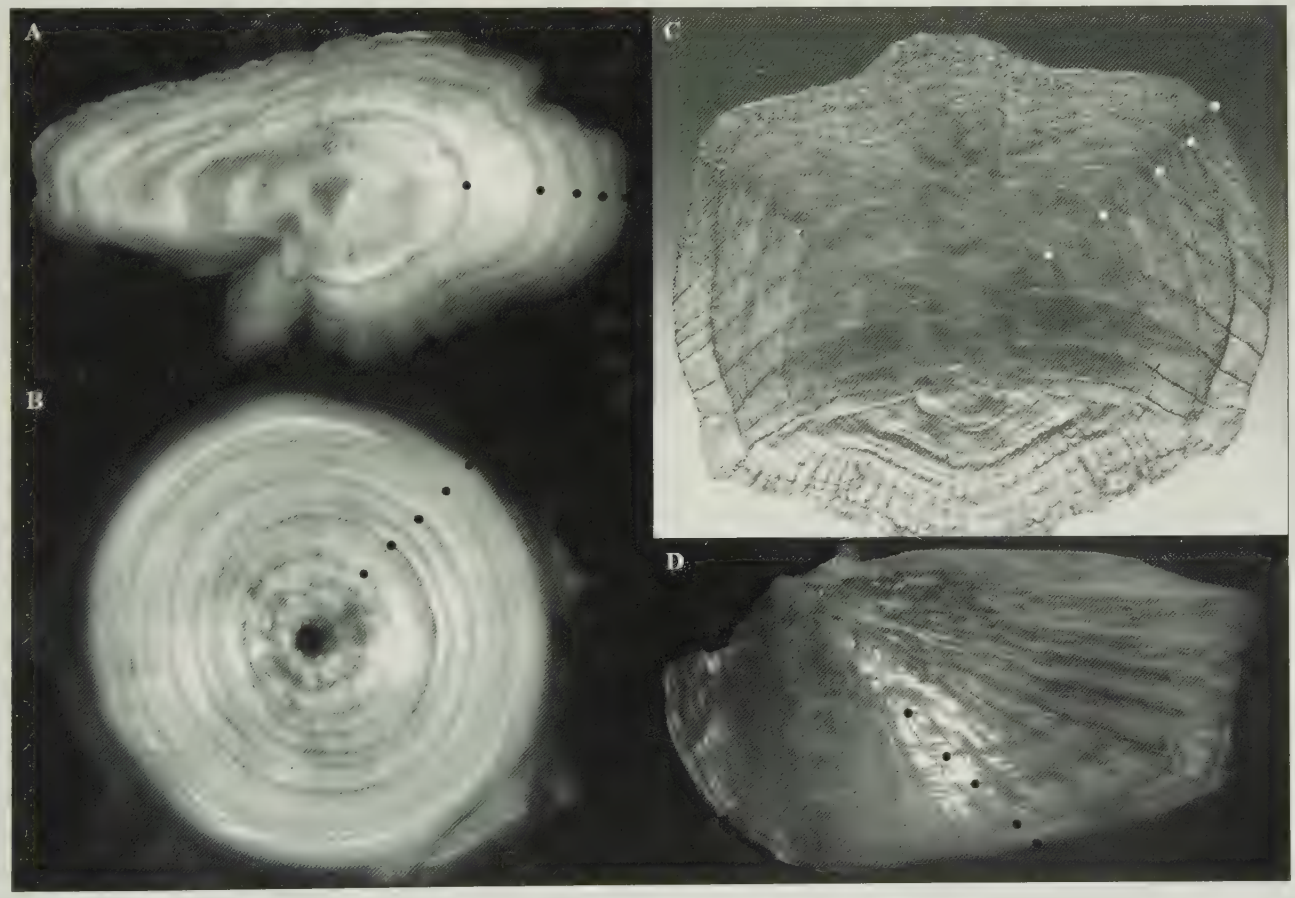

Figure 1

Images of an (**A**) otolith, (**B**) vertebra, (**C**) scale, and (**D**) operculum from a 5-year-old male American shad (*Alosa sapidissima*) that was captured on 31 May 2010 in the Merrimack River in Lawrence, Massachusetts. The dots on each image indicate locations of presumed annuli. This fish was captured during the spawning season, which is also the period of annulus deposition; therefore, the edge is counted as the fifth annulus.

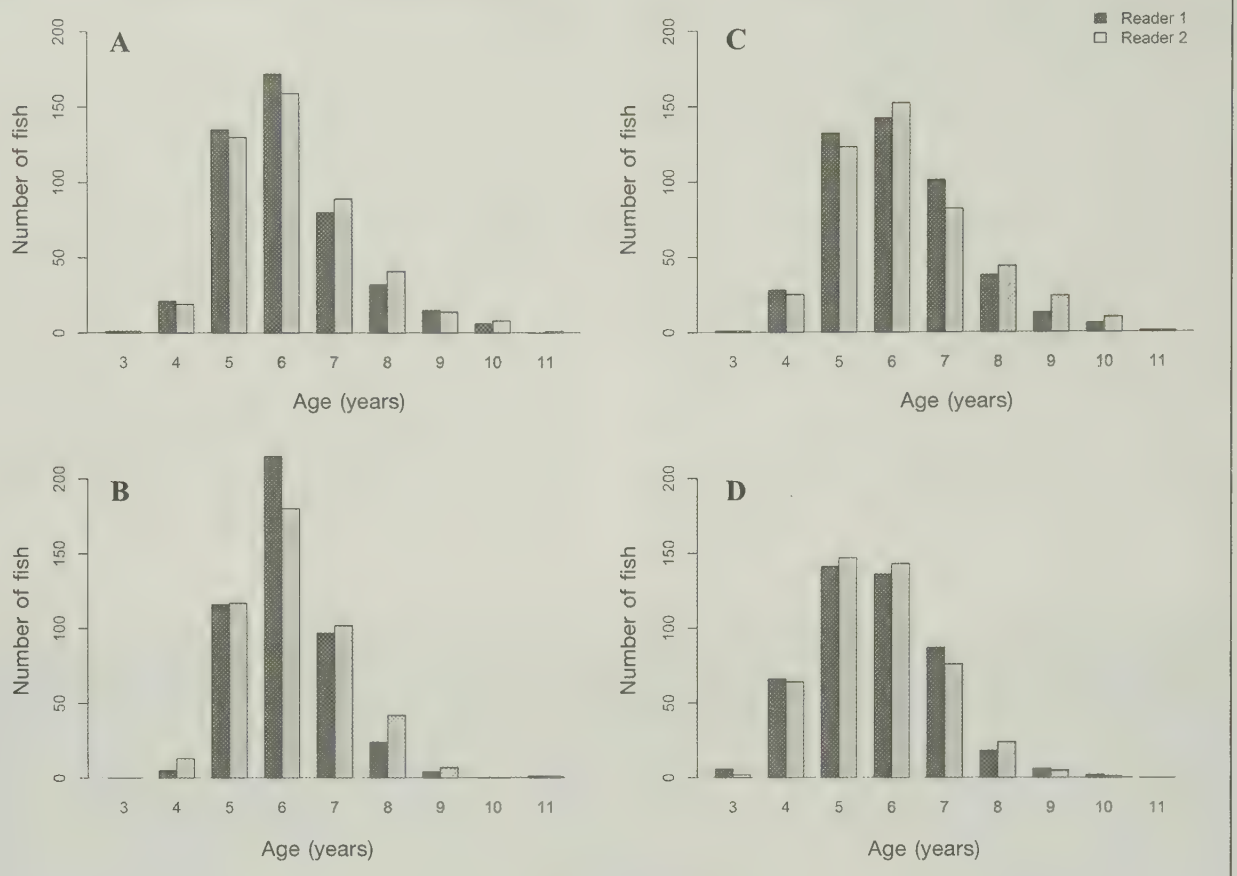

Figure 2

The age structure of the 462 American shad (*Alosa sapidissima*) collected during May–June in 2008–2010 from the Merrimack River in Lawrence, MA, from annuli in (**A**) otoliths, (**B**) scales, (**C**) vertebrae, and (**D**) opercula. Annuli were counted by each of 2 readers.

Results

For this study, 545 American shad were collected. Only 462 fish (283 males, 179 females) were deemed readable for all 4 structures and, therefore, these fish were included in our analyses. Fish with TLs from 401 to 639 mm (average=502 mm) were represented. Average TL was longer for females than for males (518 versus 477 mm TL).

All 4 structures that were examined contained annual marks (Fig. 1), but otoliths and vertebrae showed the most defined marks. American shad in this study ranged in age from 3 to 11 years. The majority of fish were age 5 and 6. No fish were assigned an age of 11 years with the use of opercula or 3 years with scales. Both readers found age-6 fish at a larger percentage on the basis of scale ages than they did with any other structure (Fig. 2).

Analysis of between-reader and within-reader results for each structure indicated that the most precise age readings came from otoliths: precision was measured between readers with agreement of 76.2% and a CV of 2.99% and among results from a single reader with agreement of 74% and a CV of 2.93%. The next most precise age estimates were determined from scales, with agreement of 66.9% and a CV of 4.28% between readers and agreement of 65% and a CV of 5.1% within results for a reader. Aging with vertebrae resulted in the third-most precise readings, followed by age analysis with opercula (Table 1). Within-reader comparisons were made between otolith ages and ages determined from the other structures. Vertebral ages matched the otolith ages most closely for reader 1 (55.6%). Vertebra and scale ages both agreed 53.2% of the time with otoliths for reader 2. The CV for both readers was better between otoliths and vertebrae (5.95% and 6.39%) than between otoliths and scales (6.87% and 6.63%). Agreement between opercula and otoliths was the worst for both readers (Table 1).

In comparisons of results between readers and within reader 2, at least 93% of all age disagreements were within 1 year. For both readers, agreement between ver-

Table 1

The precision of age estimates obtained from otoliths, scales, vertebrae, and opercula of American shad (*Alosa sapidissima*) was tested between readers, within results for a single reader for a subsample of 100 fish, and between structures for each reader. All samples were collected in May and June during 2008–10 from the Merrimack River in Lawrence, Massachusetts. The percent agreement and coefficient of variation (CV) are presented for each comparison.

		Agreement (%)	CV (%)
Between readers	Otolith	76.2	2.99
	Scale	66.9	4.28
	Vertebra	63.4	4.59
	Operculum	49.8	7.07
Within reader 2	Otolith	74.0	2.93
	Scale	65.0	5.10
	Vertebra	56.0	5.96
	Operculum	49.0	7.32
Reader 1	Otolith vs. scale	50.6	6.87
	Otolith vs. vertebra	55.6	5.95
	Otolith vs. operculum	34.0	9.80
Reader 2	Otolith vs. scale	53.2	6.63
	Otolith vs. vertebra	53.2	6.39
	Otolith vs. operculum	34.2	9.52

Table 2

American shad (*Alosa sapidissima*) collected in May and June during 2008–10 from the Merrimack River in Lawrence, Massachusetts, were aged by 2 readers using otoliths, scales, vertebrae, and opercula. The percent agreement between readers, within results for a single reader for a subsample of 100 fish, and between structures for each reader is shown as exact agreement (±0), within 1 year (±1), 2 years (±2), and 3 years (±3).

		±0	±1	±2	±3
Between readers	Otolith	76.2	97.6	99.8	100.0
	Scale	66.9	95.9	99.4	100.0
	Vertebra	64.3	95.9	98.9	100.0
	Operculum	49.8	93.5	98.9	99.8
Within reader 2	Otolith	74.0	100.0	100.0	100.0
	Scale	65.0	96.0	99.0	100.0
	Vertebra	56.0	96.0	98.0	100.0
	Operculum	49.0	93.0	99.0	100.0
Reader 1	Otolith vs. scale	50.6	90.9	98.3	99.6
	Otolith vs. vertebra	55.6	93.3	99.4	100.0
	Otolith vs. operculum	34.0	86.8	97.8	99.8
Reader 2	Otolith vs. scale	53.2	89.4	98.3	99.8
	Otolith vs. vertebra	53.2	92.0	99.1	99.8
	Otolith vs. operculum	34.2	87.0	98.7	99.4

tebral ages and otolith ages was within 1 year (93.9% and 92%) and 2 years (99.4%, 99.1%), results that are better than the agreement between scale ages and otolith ages (1 year: 90.9% and 89.4%; 2 years: 89.3% and 89.3%). More than 99% of all age disagreements were within 3 years (Table 2).

Wilcoxon rank sum tests between readings from otoliths and those from other structures showed that both readers significantly overestimated the ages of age-4 and age-5 fish when they used scales and vertebrae. Both readers also underestimated the ages of fish age 6 and older with the use of opercula, as well as ages of fish age 7 and older with the use of scales (Table 3; Fig. 3). Although significance was not tested for age-3 or age-11 fish, because of a sample size of 1 for each age, the limited data for these 2 fish indicate that the trends outlined previously continue into these ages.

Discussion

On the basis of the presence of strong annular marks on otoliths as well as the lowest CV and the highest percent agreement between readers and within readers for readings from otoliths in this study, the otolith was deemed the best structure for determining the age of American shad. Furthermore, using fish marked with oxytetracycline as did Hendricks et al. (1991), Duffy et al. (2012) were able to validate the accuracy of aging American shad with the use of otoliths. Additionally, otoliths are moderately easy to remove and require less preparation for aging than any of the other structures examined.

The vertebra was the second-most preferred structure for aging American shad. When compared with otolith ages, vertebral ages were less biased than scale or operculum ages. In a study similar to ours, Yilmaz and Polat (2002) compared the precision of age estimates from otoliths, vertebrae, opercula, subopercula, and scales from pontic shad and found that the most precise aging was performed with vertebrae. However, Višnjić-Jeftić et al. (2009) found that the precision of aging the pontic shad was dependent more on the experience of the reader than on the structure being aged. Readers in our study had minimal prior experience in aging vertebrae. Therefore, with practice for readers, vertebral ages for American shad could approach the level of precision seen with otolith ages. However, the work to remove and process vertebrae was more labor-intensive than the effort required for otoliths, and there-

Table 3

American shad (*Alosa sapidissima*), collected in May and June during 2008–10 from the Merrimack River in Lawrence, Massachusetts, were aged by 2 readers. Each reader used otoliths, scales, vertebrae, and opercula to determine the age of each fish. The average age assigned to each structure for each otolith age is shown. An asterisk (*) denotes significant differences (P<0.05) from the otolith ages determined with Wilcoxon rank sum tests. Significance was not tested for ages 3 and 11 because of insufficient sample size (n).

Otolith age	Vertebra	Scale	Operculum	n
Reader 1				
3	3.00	4.00	3.00	1
4	*4.48	*4.95	4.10	21
5	*5.29	*5.53	4.98	135
6	5.99	6.09	*5.73	172
7	6.88	*6.63	*6.30	80
8	7.84	*7.00	*7.00	32
9	*8.40	*7.07	*7.20	15
10	9.50	*7.83	*7.83	6
Reader 2				
3	3.00	5.00	3.00	1
4	*4.68	*4.74	4.26	19
5	*5.25	*5.42	4.93	130
6	6.03	6.09	*5.65	159
7	7.00	*6.72	*6.22	89
8	7.71	*7.29	*6.85	41
9	8.86	*7.36	*7.71	14
10	9.63	*8.13	*7.63	8
11	10.00	8.00	7.00	1

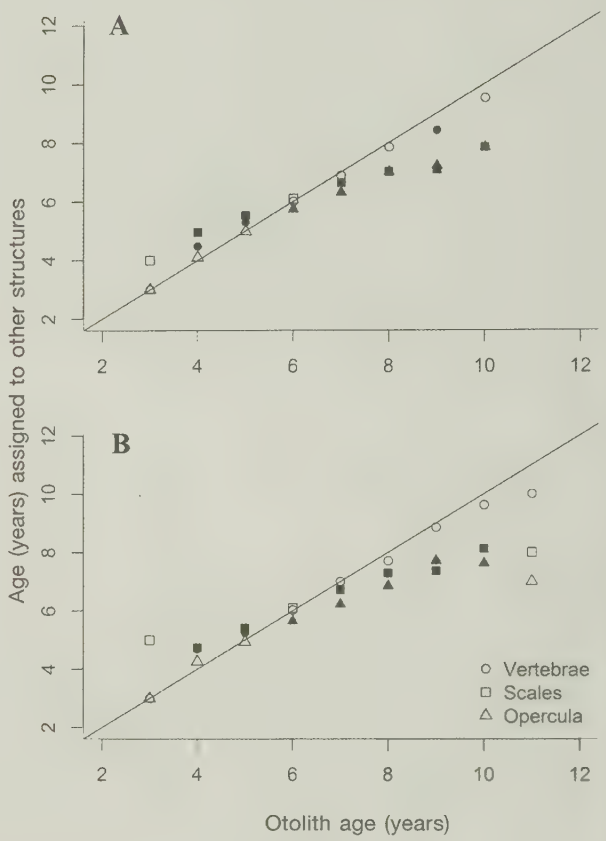

Figure 3

Ages from otoliths of American shad (*Alosa sapidissima*) collected in May and June during 2008–2010 from the Merrimack River in Lawrence, Massachusetts, compared with the average ages assigned through the use of vertebrae, scales, and opercula by (**A**) reader 1 and (**B**) reader 2. The diagonal line represents agreement with otoliths. Filled symbols represent ages that are significantly different (P<0.05) from ages from otoliths; empty symbols are not. Significance was tested with Wilcoxon rank sum tests for ages 4–10. Significance was not tested for ages 3 or 11 because of a sample size of 1 for each age.

fore the vertebra is a less ideal structure for production aging.

In this study, age estimates obtained from scales of American shad were not as precise as those produced from otoliths and were more biased toward underaging older (≥7 years) fish than were age estimates obtained from vertebrae. For these reasons, the scale is not viewed as a preferred aging structure. The use of scales for age determination had the advantage of being the only nonlethal method tested in this study. However, we found that many scales were regenerated and, therefore, not suitable for age determination. Although scales can provide data regarding repeat spawning behavior (Cating, 1953), information that is used in the management of the American shad (ASMFC[2]), the spawning marks left by reabsorption of the scale margin during a freshwater spawning run (Cating, 1953) can hinder the use of scales for accurate age determination. If enough of the scale is reabsorbed, annuli laid down in previous years can be very difficult to interpret.

The results of our study agree with the findings of McBride et al. (2005) that indicate that scales produce biased ages, where readers tend to over-age young (≤5 years) fish and under-age older fish. Furthermore, Upton et al. (2012) showed a 50% error in scale ages of American shad of known age. This trend of otoliths providing better precision and a larger range of ages than those provided by scales has been shown in several other species as well (Barnes and Power, 1984; Welch et al., 1993; Secor et al., 1995; Sipe and Chittenden, 2001; Zymonas and McMahon, 2009).

Opercula resulted in the least reliable readings in this study of aging structures for American shad. Opercula were difficult to read, required more processing than scales or otoliths, and provided estimates of the lowest precision compared with results from the other structures examined. Contrary to the findings of

Yilmaz and Polat (2002) with pontic shad, we did not find annuli easy to distinguish in opercula of the American shad, especially in older (≥6 years) fish. Furthermore, our ages determined from opercula were biased compared with ages derived from otoliths, leading to fish of age 5 and older being under-aged.

The results of this study support the use of otoliths for age determination of American shad. Ages estimated from otoliths were more precise (between and within readers) than ages derived from any of the other structures examined. Campana (2001) suggested a CV of 5% or less is ideal for a species of moderate longevity. In this study, only ages from otoliths achieved a CV of less than 5% between and within readers. Ages estimated from scales and vertebrae were higher in young (≤5 years) fish than ages determined from otoliths. Furthermore, ages estimated from scales and opercula were lower than ages from otoliths in older (≤7 years) fish. If possible, a reference collection of otoliths should be compiled for each region for which age estimates would be useful. Such a collection could provide a valuable tool for training inexperienced readers of annuli, as well as would prevent a long-term drift for age estimates determined by experienced personnel (Campana, 2001).

Acknowledgments

We would like to thank the employees of the Massachusetts Division of Fisheries and Wildlife that helped sample American shad at the Essex dam in Lawrence. We also thank S. Turner for her help in processing samples. We also appreciate the thorough comments provided by M. Armstrong and G. Nelson on revisions at the manuscript stage. Funding for this project was provided, in part, through the Wildlife and Sport Fish Restoration Program of the U.S. Fish and Wildlife Service (Massachusetts Sport Fish Restoration Grant F-68-R).

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Slipper lobsters (Scyllaridae) off the southeastern coast of Brazil: relative growth, population structure, and reproductive biology

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Abstract—The hooded slipper lobster (*Scyllarides deceptor*) and Brazilian slipper lobster (*S. brasiliensis*) are commonly caught by fishing fleets (with double-trawling and longline pots and traps) off the southeastern coast of Brazil. Their reproductive biology is poorly known and research on these 2 species would benefit efforts in resource management. This study characterized the population structure of these exploited species on the basis of sampling from May 2006 to April 2007 off the coast of Santos, Brazil. Data for the absolute fecundity, size at maturity in females, reproductive period, and morphometric relationships of the dominant species, the hooded slipper lobster, are presented. Significant differential growth was not observed between juveniles and adults of each sex, although there was a small investment of energy in the width and length of the abdomen in females and in the carapace length for males in larger animals (>25 cm in total length [TL]). Ovigerous females were caught more frequently in shallow waters in August–September than in January–February, indicating a possible migration to spawn. Fecundity ranged from 55,800 to 184,200 eggs (mean fecundity: 115,000 [standard deviation 43,938] eggs). The spawning period occurred twice a year, with a higher relative frequency between July and October, and the length at 50% maturity for females was ~25 cm TL; both these findings should be considered by resource managers. Proper management of catches of slipper lobsters is important because of the high economic value of this fishery.

Manuscript submitted 18 June 2013.
Manuscript accepted 2 December 2014.
Fish. Bull. 113:55–68 (2015).
doi: 10.7755/FB.113.1.6

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

Few species-specific fisheries worldwide exist for the slipper lobsters (Scyllaridae), in contrast to those for the spiny lobsters (Palinuridae) and clawed lobsters (Nephropidae), although some slipper lobsters have significant commercial value (Spanier and Lavalli, 2007; Duarte et al., 2010). According to Holthuis (1991), of the 85 species of lobsters recorded (see Lavalli and Spanier, 2007), 35.3% are of commercial interest, and of these interest has increased in species of the genus *Scyllarides*, such as the Brazilian slipper lobster (*S. brasiliensis*), Mediterranean slipper lobster (*S. latus*), and blunt slipper lobster (*S. squammosus*). In addition, other species of Scyllaridae have commercial value, including 4 species of the genus *Ibacus*, the velvet fan lobster (*I. altricrenatus*), Japanese fan lobster (*I. ciliatus*), smooth fan lobster, (*I. novemdentatus*), and butterfly fan lobster (*I. peronii*), as well as the sculptured mitten lobster (*Parribacus antarcticus*) and flathead lobster (*Thenus orientalis*).

The reproductive biology of members of the Scyllaridae (Lavalli and Spanier, 2007) has been studied for the genera *Thenus* (Kagwade and Kabli, 1996; Courtney et al., 2001) and *Ibacus* (Stewart et al., 1997; Haddy et al., 2005) with emphasis on the genus *Scyllarides* (Hardwick and Cline, 1990; Spanier and Lavalli, 1998; DeMartini and Williams, 2001; DeMartini et al., 2005; Hearn and Toral-Granda, 2007; Oliveira et al., 2008). According to the above mentioned authors, the sizes of females at maturity are smaller in species of the genera *Ibacus* (butterfly fan lobster) and *Thenus* (flathead lobster and *T. indicus*) than in species of the genus *Scyllarides* (blunt slipper lobster, Galapagos slipper lobster [*S. astori*], and hooded slipper lobster [*S. deceptor*]). Moreover, species of *Iba-*

cus and *Thenus* show lower fecundity than species of *Scyllarides*.

A new, species-specific study for the hooded slipper lobster is needed to gain a better understanding of biological patterns in this species. The variability in the reproductive biology of species of *Scyllarides* has been shown to be relatively high. For example, the hooded slipper lobster has 2 spawning seasons per year (Oliveira et al., 2008)—a difference from the Galapagos slipper lobster (Hearn and Toral-Granda, 2007)—and a mean tail width at maturity of 62.6 mm (Oliveira et al., 2008), compared with a mean tail width of 47.6 mm for the blunt slipper lobster (DeMartini et al., 2005). Studies of *Scyllarides* species are needed to estimate size at sexual maturity, fecundity, and reproductive period and to determine locations that are favorable for spawning in order to better understand the life cycle of these species and, therefore, to improve fisheries management toward a more sustainable resource (Sparre and Venema, 1998; Chubb, 2000).

Chace (1967) reported that a population of the red slipper lobster (*S. herklotsii*) supported an intense fishing effort at Saint Helena (South Atlantic), and DeMartini and Williams (2001) noted that the blunt slipper lobster accounted for 64% of the lobster catch at Maro Reef (Northwestern Hawaiian Islands). Species of Scyllaridae also are targeted by other fisheries (e.g., in the Mediterranean Sea, Australia, the Galapagos Islands, India, and Australia); however, the numbers of fisheries landings from lobster catches have declined rapidly worldwide, and fisheries failures have occurred or are likely to occur in the near future (Lavalli and Spanier, 2007; Spanier and Lavalli, 2007). Studies show that generally in several places in the world most fisheries that have targeted slipper lobsters lacked effective regulations for the conservation of stocks and the economic maintenance of local fisheries (Lavalli and Spanier, 2007). A similar situation exists in Brazil, where there are no regulations that govern the extraction of these resources and where there is little specific knowledge about the basic biology of these species.

In Brazil, there are 3 genera of Scyllaridae: *Scyllarus*, *Parribacus,* and *Scyllarides*. Two species of *Scyllarides* occupy the south and southeast: 1) the Brazilian slipper lobster, distributed at depths of 20–130 m from Antilles to Brazil (Maranhão to São Paulo), and 2) the hooded slipper lobster, distributed at depths of 6–420 m from Argentina to Brazil (Rio de Janeiro to Rio Grande do Sul) (Holthuis, 1985, 1991; Melo, 1999; Oliveira et al., 2008; Duarte et al., 2010). Brazilian slipper lobsters are caught by 2 kinds of commercial fishing fleets in southeastern Brazil: 1) medium-size double trawlers that target mostly shrimp and 2) pot-and-trap fleets that target the common octopus (*Octopus vulgaris*). The lobsters caught by these fleets are traded intact (whole). Species of *Scyllarides* are not the main target of the majority of the fisheries off southeastern Brazil. In the same region, Duarte et al. (2010) have shown a significant reduction in the abundance of the hooded slipper lobster despite a relatively low fishing effort. This reduction can be explained by its slow rate of population growth, high total mortality (Duarte et al., 2011), and late maturity (Oliveira et al., 2008) compared with other species of the same family. Also, traders have noted a smaller size of individuals in the catch in recent years (Duarte et al., 2011).

Brazil currently has no fishery management legislation that regulates the extraction of slipper lobsters in its waters, and data on the reproductive biology of these species of Scyllaridae would provide important life-cycle information that could be used for decision-making. Therefore, the aims of this study were to describe the relative growth (biometrics) and reproductive biology (maturity, reproductive period, fecundity, and spawning sites) of the hooded slipper lobster. We also sought to identify different population strata by sex, size, fishing area, and coloration of the carapace and to contribute the resulting data to inform future management recommendations that would promote sustainability and conservation of this species in commercial fisheries.

Materials and methods

Data collection on land

Weekly monitoring (through visits to landing sites) and 2 or 3 sampling efforts during the year were conducted for this study from May 2006 to April 2007 at all the industrial landing sites in the State of São Paulo, Brazil (at the sites of these 7 companies: 1) Cooperativa Mista de Pesca NIPO Brasileira, 2) Aliança, 3) Franzese, 4) Itafish, 5) Balãn, 6) TPPS-Santos, and 7) Araripe[1]). About 70% of all the fishing landings that occurred in this study period were monitored, and, of the 100 fishing landings that were monitored, 72 landings were from medium-size double trawlers and 28 landings were from the pot-and-trap fleet (Instituto de Pesca, Governo do Estado de São Paulo, ProPesq, http://www.pesca.sp.gov.br/estatistica.php). As part of this monitoring, the total catch of hooded slipper lobster and information about the fishing areas (depth, latitude, and substrate type) were recorded.

The double trawler vessels have 2 identical semiconical nets. The vertical opening of each net is created by a flotation device from a headrope 20.0 m in length, each mouth opening is 15.0 m wide by 1.5 m high, and trawl doors (weighing 60–80 kg) keep the net open. The majority of these vessels preserve their catch on board with ice (see illustrations in Duarte et al., 2010).

Fishing vessels that target common octopus have refrigerators for storage of their catch (Castanhari and Tomás, 2012). Each of these vessels can include up to

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

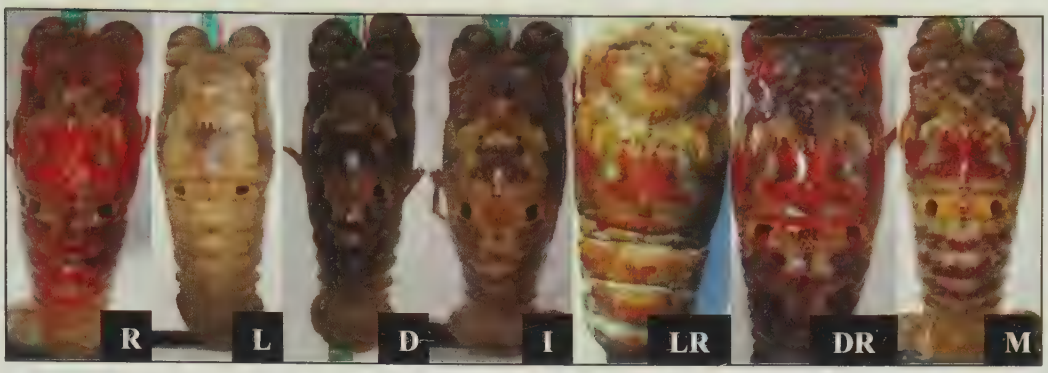

Figure 1

Carapace color patterns established for specimens of the hooded slipper lobster (*Scyllarides deceptor*) observed at fishery landings in southeastern Brazil from May 2006 to April 2007: red (R), light (L), dark (D), intermediate (I), light red (LR), dark red (DR), and mixed (M).

10 longlines with 2500 pots and 150 interspersed traps per longline, providing a total of 25,000 pots and 1500 traps for an individual fishery. The traps are baited (with remains of fishes) to catch octopuses, fishes, and slipper lobsters, and the pots are not baited, (Duarte et al., 2010; Castanhari and Tomás, 2012). Pots have a minimum internal diameter of 15 cm and are used as a shelter by common octopus. The number of pots cannot exceed 20,000 units per boat, and baited pots are not permitted with this type of fishing (SEAP, 2005) (see trap differences in Duarte et al., 2010). Lobsters are not caught in these pots.

Slipper lobster species were identified in this study by examination the morphological structure of the posterior margin of the 2nd abdominal pleura (Melo, 1999), which is a large concave spine in the hooded slipper lobster and straight or slightly convex in the Brazilian slipper lobster. Sex of lobsters was determined by the location of the gonopores on the base of the 3rd or 5th pair of pereiopods in males and females, respectively (Abele, 1982; Hardwick and Cline, 1990).

Sampling efforts conducted at landing sites during the study period resulted in the collection of 1032 specimens, which were measured for biometric relationships and size structure with a tape measure attached to a wooden board for total length (TL), with a caliper for other linear measurements, and with a manual balance for the total weight (Abele, 1982). With a tape measure, TL was measured in centimeters from the distal tip of the antenna to the posterior end of the telson. The following measurements were obtained in millimeters with a caliper: carapace length (CL) between the distal extremity of the rostrum to the posterior margin of the carapace; carapace width (CW) between the sides of the carapace at its midpoint; abdomen width (AW) between the sides of the 1st and 2nd abdominal somites; abdomen length (LA) between the posterior margin of the carapace and the posterior end of the telson; and antenna length (AL) from the base to the distal tip. The total weight (Wz) was measured in grams by weighing the intact, fresh animal.

The carapace color of each specimen was recorded upon landing and was classified according to 7 patterns (Fig. 1), 3 of which were established by the predominant color (>75%): red (R), light (L), and dark (D). The remaining 4 patterns were classified by their color tone. For 3 of the remaining patterns, ~50% of a carapace had to have an intermediate (I), light red (LR), or dark red (DR) tone; for the fourth pattern, ~33.3% of a carapace had to have a mixed (M) tone.

All the ovigerous females (100%, n=22) were recorded and collected during the sampling efforts from May 2006 to April 2007. During the study period, this subsample of 22 female specimens, with lengths that ranged from 22.5 to 32.0 cm TL, were collected from different boats, and their stage of embryonic development was categorized according to the classification of DeMartini and Williams (2001). The animals were placed in individual plastic bags and kept in crushed ice before laboratory analysis.

Laboratory processing

Females also were collected at the time of landing and were later dissected for macroscopic examination of their gonads, which were categorized according to the classification proposed by Stewart et al. (1997) and Haddy et al. (2005). This classification was established for lobster species from the genus *Ibacus* and is also valid for the species in our study because of identical macroscopic characteristics. Five maturation stages were established: the first 2 stages for juvenile individuals and stages 3–5 for mature individuals. At stage 1, the ovary is small, narrow, translucent to white, and has no visible oocytes. A female at stage 2 has a small and cream to yellow ovary with no visible oocytes. At

stage 3, the ovary is developed, has a small volume and is orange, and has visible oocytes at the ovary wall. At stage 4, the ovary is largely inflated, fills the whole carapace cavity, and is bright orange, with oocytes clearly visible along the ovary wall. Finally, at stage 5, the ovary is developed but has a flaccid appearance and is cream to yellow; there may still be some oocytes on the ovary wall—a specific peculiarity of this stage.

Individual fecundity was quantified volumetrically (Vazzoler, 1996) by using females with eggs in the early stages of embryonic development (orange in color). This method avoided underestimation caused with females at later stages, when there was the possibility of loss of eggs with catching and handling, or early larval hatching (DeMartini and Williams, 2001). The laboratory protocols were the same as those of Vazzoler (1996); eggs were removed from pleopods by dissociation in 10% NaClO, and were then vigorous stirred. The oocytes from each egg mass were transferred to a 1-L beaker and homogenized with a glass rod, and seven 5-mL subsamples were removed with a pipette. The oocytes were placed in gridded petri dishes for counting under a stereomicroscope (20×). We estimated individual fecundity (F) according to the method proposed by DeMartini and Williams (2001), counting the number of eggs in subsamples, discarding the extreme values (minimum and maximum), and calculating the mean individual fecundity of the 5 remaining subsamples (fs) with the following equation:

$$F = (tv \times fs) \; / \; dv, \tag{1}$$

where tv = total volume of the egg mass with a dilution of 1 L; and
dv = the dilution volume of the egg subsample or 5 mL).

The relationship of TL to the number of eggs (NE) was calculated with the following equation:

$$NE = (b \times TL) - a, \tag{2}$$

where a = the intercept; and
b = the slope of linear regression.

Data analysis

The statistical analyses for this study were performed with R software, vers. 2.13.0 (R Development Core Team, 2011) (Ihaka and Gentleman, 1996), and the fisheries were mapped with the Surfer contouring and 3-D mapping package, vers. 8 (Golden Software, Golden, CO). We adopted the TL as the size indicator for the hooded slipper lobster, as was done in previous studies of lobsters of the genus *Scyllarides* (Hearn, 2006; Pessani and Mura, 2007).

The relative growth of each sex was assessed by a regression analysis of the empirical points for morphometric relationships given by the power function $y=ax^b$, and then a t-test was used to check for possible differences in allometry (Huxley, 1950). The following morphometric relationships were evaluated: AL×TL, CL×TL, LA×TL, AW×TL, CW×TL and W×TL (Abele, 1982). These relationships indicated the possible differences between the linear regressions obtained for each sex by comparisons with an analysis of covariance of constants a and b in the linear regressions of the biometric relationships (Zar, 1999; Faraway, 2002).

To represent the allometric relationships from the power function in a linear form, the dependent (y-axis) and independent (x-axis) variables were transformed by natural logarithms (ln). This transformation,

$$\ln y = \ln a + (b \times \ln x), \tag{3}$$

facilitates the use of a least squares fitting technique with linear regression:

$$y = a + (b \times x). \tag{4}$$

This mathematical procedure transforms the curvilinear relationship into a linear equation or equations and enables graphic comparisons of linear growth phases for the evaluation of biometric distinctions between developmental stages (juvenile and adult). Therefore, the linearized data ($\ln y=\ln a+[b\times\ln x]$) for each relationship were assessed with the segmented library (Muggeo, 2008) in R (vers. 2.13.0) to identify significantly different growth rates during ontogeny, according to procedures used by Pardal-Souza and Pinheiro (2012). This method of regression analysis seeks to partition the independent variable into intervals at break points, separating line segments that are fitted to each interval. The mean length at which 50% of females reached maturity (L_{50}) was estimated, under sigmoid adjustment, from the proportion of individuals with mature gonads (females in stages 3–5) in size classes of 1 cm TL (Hovgard and Lassen, 2000):

$$P = 1 \; / \; (1 + e^{-r(L - L_{50}')}), \tag{5}$$

where P = the probability that a female is mature;
r = the slope;
L_{50} = the mean TL where the probability of mature females is 50%; and
L = the mean TL.

Data on the carapace color were analyzed in relation to size class, sex, the area of capture, and fishing gear. Five major fishing areas were established by mapping the fishing grounds of 2 types of vessels with different storage types (double trawlers that store their catch on ice and vessels that use pots and traps and store catch in refrigerators) on the basis of their similar latitudes and depths of fishing grounds for lobster species. Size composition and sex also were evaluated by fishing area, season, and month of capture. Size distribution was compared between sexes by using a t-test (Zar, 1999). An analysis of variance was used, separately for each variable, to evaluate the occurrence of different color patterns by sex (exclusivity or predominant patterns), fleet (differences in storage type), capture period (month and season), and fishing area, as well as to

Table 1

Morphometric relationships for the hooded slipper lobster (*Scyllarides deceptor*) sampled from May 2006 through April 2007 from pot-and-trap and double-trawler fleets that operate off southeastern Brazil. Data include results from mathematical equations (power function and log transformation), adjustments (coefficient of determination [r^2]), and analysis of covariance between the regressions of each biometric relation and allometric representation with 5% significance (*t*-test). AL=antenna length; LA=abdomen length; CL=carapace length; TL=total length; abdomen width=AW; CW=carapace width; W=weight; 0=isometric growth (b=1); +=positive allometric growth (b>1); −=negative allometric growth (b<1); M=males; and F=females. The relationship of the weight of animals was compared with the value 3 for b from the morphometric analysis. Significance codes: ns=P>0.05; *=P<0.05; **=P<0.01; and ***=P<0.001.

Morphometric relation	Sex	n	Power function $Y = ax^b$	Power function (linear form) $\ln y = \ln a + (b \times \ln x)$	r^2	Intercept (a)	Slope allometry (b)	(P<0.05)
AL×TL	M	189	$AL=0.243\ TL^{0.973}$	$\ln AL=-1.48+0.973\ \ln TL$	0.85	0.021	0.111	0
	F	184	$AL=0.281\ TL^{0.944}$	$\ln AL=-1.27+0.944\ \ln TL$	0.92	*	ns	−
CL×TL	M	191	$CL=0.515\ TL^{0.919}$	$\ln CL=-0.664+0.919\ \ln TL$	0.92	0. 006	0.626	−
	F	182	$CL=0.470\ TL^{0.934}$	$\ln CL=-0.755+0.934\ \ln TL$	0.97	**	ns	−
LA×TL	M	190	$AL=0.339\ TL^{1.054}$	$\ln AL=-1.081+1.054\ \ln TL$	0.89	0.0002	0.352	0
	F	184	$AL=0.321\ TL^{1.068}$	$\ln AL=-1.14+1.067\ \ln TL$	0.97	***	ns	+
AW×TL	M	163	$AW=0.312\ TL^{0.951}$	$\ln AW=-1.16+0.951\ \ln TL$	0.93	$<2.10^{-16}$	0.066	0
	F	171	$AW=0.269\ TL^{0.986}$	$\ln AW=-1.31+0.986\ \ln TL$	0.93	***	ns	0
CW×TL	M	272	$CW=0.653\ TL^{0.869}$	$\ln CW= -0.427+0.869\ \ln TL$	0.9	0.225	0.376	−
	F	266	$CW=0.657\ TL^{0.868}$	$\ln CW=-0.419+0.868\ \ln TL$	0.95	ns	ns	−
	Total	538	$CW=0.655\ TL^{0.860}$	$\ln CW=-0.401+0.864\ \ln TL$	0.94	−	−	−
W×TL	M	392	$W=0.0644\ TL^{2.73}$	$\ln W=-9.037+2.73\ \ln TL$	0.93	0.289	$<2.10^{-16}$	−
	F	437	$W=0.0771\ TL^{2.67}$	$\ln W=-8.707+2.67\ \ln TL$	0.93	ns	***	−

evaluate the size of the specimens by sex. Interactions between variables were not evaluated. In all cases, the means were compared by a posteriori multiple comparison with Tukey's honestly significant difference test (Zar, 1999; Faraway, 2002). The chi-square (χ^2) test was used to evaluate whether the sex ratio was different from 1:1 in samples with a sample size (n) ≥10 individuals (Zar, 1999), depending on the month, season, size class (TL, measured in centimeters), fishing gear, and fishing area.

Results

Distributions of fishing cruises and specimens caught

Of the 72 landings by 25 double trawlers that operated at depths of 40–220 m between the latitudes 23°20′S and 26°13′S during the study period from May 2006 to April 2007, 51.4% contained specimens of the hooded slipper lobster. Lobster occurred in 100% of the 28 landings of the pot-and-trap fleet, which operated at depths of 43–180 m and at latitudes between 23°30′S and 27°00′S.

During the study period, 1029 specimens were counted, with most obtained by the pot-and-trap fleet (65.2%) rather than by double trawlers (34.8%). The hooded slipper lobster was abundant during all months of the study period. A small number of specimens of the Brazilian slipper lobster were captured in April 2007 from a single double trawler landing from a depth between 45 and 130 m farther north in the study area (from 23°30′S, 43°00′W to 24°19′S, 45°09′W).

Relative growth

All the morphometric relations showed a coefficient of determination (r^2) with values between 0.85 and 0.97 (Table 1). The relation AL×TL (females), as well as the relations of CL×TL, CW×TL, and W×TL (both sexes), showed a negative allometry of the dependent variables in relation to body size (TL) of hooded slipper lobster. The allometric growth was positive only for the relation LA×TL (females) (b>1), indicating a higher growth rate of the dependent variable in relation to the body size of this sex. For other cases, the growth was isometric (b=1), indicating no change in growth rate between the variables during ontogeny. However, no inflection (or break point) was observed during the segmentation analysis of the regression lines, indicating no significant morphometric differences between juveniles and adults for both sexes of the hooded slipper lobster.

In the analysis of covariance (Table 1), the linear growth phases of juveniles and adults were observed to be similar between the sexes in the CW×TL linear equations and could be grouped for the total number of individuals of both sexes combined. This phenomenon was not observed for the other relationships (AL×TL,

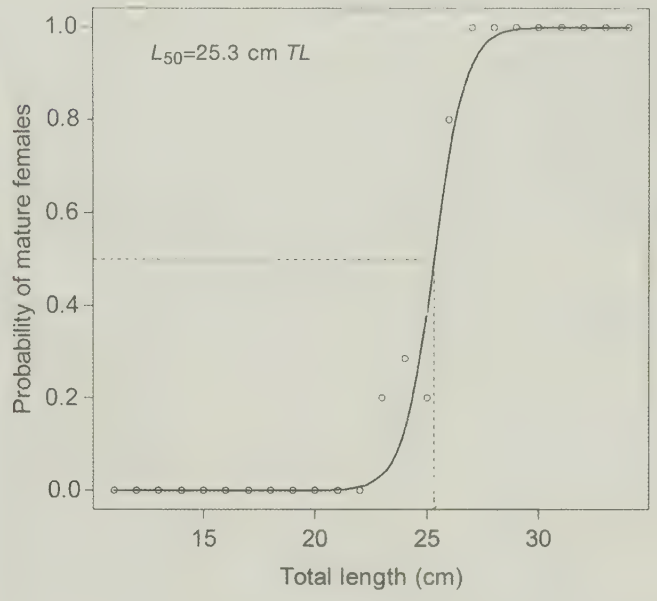

Figure 2

Estimation of mean size at 50% maturity (L_{50}), measured in total length (TL), of female hooded slipper lobster (*Scyllarides deceptor*) caught by pot-and-trap and double-trawler fleets off southeastern Brazil in a period from May 2006 through April 2007.

CL×TL, LA×TL, and AW×TL), where statistically significant differences were detected between the indexes of origin *a* (intercept) but not between the values of *b* (slope), indicating mild sexual dimorphism. This analysis indicates that males had higher values of AL and CL than females for the same reference size (TL). The same was true for females, compared with males, with regard to LA and AW. However, the relationship W×TL differed significantly between the sexes for the value *b* in the linear regression, giving greater weight to larger males.

Reproduction

For this study, 49 female hooded slipper lobster (13.0–36.0 cm TL) were dissected, and their stages of gonad development were categorized. Of these females, 29 were classified as adults and 20 were classified as juveniles, resulting in an L_{50} of 25.3 cm TL (Fig. 2).

Only 22 ovigerous females were recorded in landings between May 2006 and April 2007 (pots and traps, n=13; double trawlers, n=9), corresponding to 11.2% of the 170 adult females caught and with sizes ranging from 22.5 to 32.0 cm TL. The spawning period occurred twice a year (Fig. 3), and a higher relative frequency occurred between July and October (60.5%) and a lower relative frequency, in January and February (7.2%).

Mean individual fecundities for 8 females (22.1–32.6 cm TL) ranged from 55,800 to 184,200 eggs. The linear relationship of number of eggs (NE) to TL (NE×TL) was

$$NE = (11{,}268 \times TL) - 183{,}361 \quad (n=8,\ r^2=0.82). \quad (6)$$

Size structure and sex ratio

The population structure of the hooded slipper lobster was very different among months as a function of TL, carapace color, fishing area, and season, both for males (Tukey's test: $3.69 \leq F \leq 9.03$; $P<0.03$) and females (Tukey's test: $33.89 \leq F \leq 101.39$; $P<0.03$). However, there were no changes in size composition (TL) as a function of fishing gear for both sexes ($P>0.101$), where sizes ranged from 14.0 to 36.0 cm TL in the double-trawler fleet and from 11.0 to 36.0 cm TL in the pot-and-trap fleet. On the basis of analysis of their individual sizes, a high percentage of females were determined to be immature (double trawlers: 65.8%; pots and traps: 68.1%), and the monthly percentage of capture of immature females ranged from

Table 2

Depths of the 5 fishing areas of the double-trawler and pots-and-trap fleets that operate off southeastern Brazil and catch hooded slipper lobster (*Scyllarides deceptor*). Standard deviations (SD) of the means are provided in parentheses.

	Depth (m)					
	Double trawlers			Pots and traps		
Fishing area	Min.	Max.	Mean (SD)	Min.	Max.	Mean (SD)
Area 1	40	100	59.9 (16.8)	70	99	89.4 (10.2)
Area 2	40	80	58.3 (13.3)	43	100	79.2 (16.8)
Area 3	41	150	100.1 (38.2)	43	68	58.8 (12.3)
Area 4	100	165	134.5 (23.9)	100	180	120.0 (31.0)
Area 5	135	220	171.6 (44.0)	–	–	–
Total	40	220	91.1 (42.3)	43	180	81.4 (18.2)

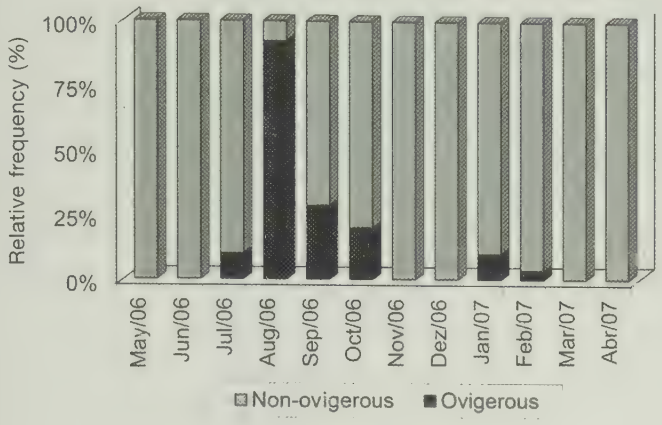

Figure 3

Relative frequency (%) of the ovigerous (black bars) and non-ovigerous female (grey bars) hooded slipper lobster (*Scyllarides deceptor*) caught each month by pot-and-trap and double-trawler fleets off southeastern Brazil from May 2006 through April 2007.

40.5% (in December) to 83.3% (in November), independent of the fishing gear used, and higher levels were recorded in trawls (84.2%) during the spring and in pots and traps (72.6%) during the winter.

Size (TL) composition showed significant monthly variation, regardless of sex ($P<0.001$), with greater differences between the monthly means for males (from 23.6 cm TL [standard deviation (SD) 3.4] in August to 19.6 cm TL [SD 2.8] in October) than for females (from 24.5 cm TL [SD 4.1 in May to 21.7 cm TL [SD 4.9] in November). No significant seasonal differences were observed in the size composition for each sex ($P=0.14$) or in the sex ratio of hooded slipper lobster ($P>0.05$). In general, the sex ratio of hooded slipper lobster (Table 3) did not differ significantly from a proportion of 1:1 ($P>0.05$), regardless of the fishing gear used ($P=0.85$). However, males predominated in smaller length classes (11.0–24.0 cm TL) and females in larger sizes (>24 cm TL). The *t*-test confirmed that females tended to be larger than males (males: 21.9 cm TL [SD 3.0]; females: 23.9 cm TL [SD 3.7]; $P<0.001$).

The spatial distribution of the fishing areas for both fleets (areas 1–5; Fig. 4; Table 2) showed that the double-trawler fleet that caught Brazilian slipper lobster operated farther south (between the latitudes 25°00′S and 26°24′S) than the pot-and-trap fleet, at depths of 40–165 m, and particularly in areas 1 and 4. On the other hand, the pot-and-trap fleet concentrated fishing efforts in shallower waters (at depths of 43–100 m), between the latitudes 24°00′S and 25°00′S, and operated preferentially in area 2.

The males from area 5 were significantly smaller than those caught in areas 2 and 4 ($P<0.01$) (Fig. 5). Females from area 5 also were smaller than females caught in areas 3 and 4 ($P<0.05$). The proportion of immature females among the adults caught in the trawl fleet ranged from 55% (area 4) to 90% (area 3), whereas, in the pot-and-trap fleet, the percentages of immature females were between 56.5% (area 2) and 75.9% (area 3).

In all fishing areas, males caught by double trawlers had a lower median size (20.7 cm TL) than males captured in pots or traps, and smaller individuals were observed in area 3. Females were more abundant in area 1 (χ^2: $P=0.036$), and males were more abundant in area 2 (χ^2: $P=0.01$).

Carapace color was used to classify 871 specimens of the hooded slipper lobster. The 7 categories evaluated were ranked in descending order (the absolute frequency for each category is shown in parentheses): D(259) > DR(247) > L(108) > R(103) > LR(91) > I(37) > M(26). The posteriori multiple comparison conducted with Tukey's test revealed significant differences between some of the color patterns for males (patterns: R≠L, I, and M; $P<0.05$) and females (patterns: R≠L, I, LR, and M; $P<0.001$). The R pattern showed the smallest variation (by size [TL]) and was characteristic of smaller individuals (mean: 21.5 cm TL [SD 2.7]), regardless of sex (Fig. 6). In addition, all females with this carapace color ($n=8$, 27.6% of immature females) were identified by dissection as juveniles, and the other color patterns were found on both juveniles and adults. Therefore, an association between R pattern and a relatively narrow range of TLs was verified for both sexes. This relationship was not affected by the sex of the lobster, fleet composition (despite differences in storage of catch), month of capture, or fishing area.

Discussion

For the hooded slipper lobster, the r^2 values for morphometric relationships showed an excellent linear correlation. Females tended to show an increase in LA, therefore, enhancing their capacity for oviposition and for hatching a greater number of eggs in the bristles of their pleopods (individual fecundity) (Stewart et al., 1997; Demartini and Williams, 2001; Oliveira et al., 2008). Although the average female is larger than the average male, it is possible that an increase in body size (TL) in males facilitates the selection, grasping, and manipulation of females at the time of copulation, as has been observed in lobsters of the genus *Panulirus* (Lavalli and Spanier, 2007). Therefore, in general, significant differential growth was not observed between the juveniles and adults of each sex, nor was there obvious sexual dimorphism, although there was a small investment of energy in the width and length of the abdomen in females and in the carapace length for males in larger animals (>25 cm TL).

Various biometric equations presented high values of r^2 and thereby reinforced their suitability for use in

Table 3

Sex ratios (male:female) of the hooded slipper lobster (*Scyllarides deceptor*) by size classes (total length [TL]) caught by double-trawler and pot-and-trap fleets off southeastern Brazil from May 2006 through April 2007. Significance codes based on chi-square test (χ^2): ns=P>0.05; * P<0.05; ** P<0.01; and *** P<0.001.

Size classes (cm TL)	Number of specimens			Sex ratio (M:F)	P (χ^2)
	M	F	Total		
11–12	1	0	1	–	–
12–13	0	0	0	–	–
13–14	2	0	2	–	–
14–15	5	0	5	–	–
15–16	12	7	19	01:00.6	0.25 ns
16–17	14	14	28	01:01.0	1.00 ns
17–18	20	19	39	01:01.0	0.87 ns
18–19	37	14	51	01:00.4	0.0013**
19–20	53	26	79	01:00.5	0.0024**
20–21	71	33	104	01:00.5	0.0002***
21–22	62	58	120	01:00.9	0.53 ns
22–23	80	46	126	01:00.6	0.0025**
23–24	59	52	111	01:00.9	0.51 ns
24–25	41	71	112	01:01.7	0.0046*
25–26	18	53	71	01:02.9	0.0327*
26–27	12	42	54	01:03.5	0.0446*
27–28	11	25	36	01:02.3	0.0196*
28–29	7	16	23	01:02.3	0.0406*
29–30	5	11	16	01:02.2	0.13 ns
30–31	3	10	13	01:03.3	0.0522 ns
31–32	2	7	9	–	–
32–33	1	3	4	–	–
33–34	0	3	3	–	–
34–35	0	1	1	–	–
35–36	0	2	2	–	–

future interconversion between size variables, particularly measures of the abdomen (LA and AW) and individual body size (TL or CL). Currently, in Brazil, some boats have begun landing only the abdomen of lobsters ("headless" lobsters)—a trend that will hamper the use of CL for monitoring this resource in the future. Total length is measured routinely and is easier for fishermen to understand compared with the other measurements of size used in this study (Sparre and Venema, 1998; Chubb, 2000).

Values of L_{50} were smaller in species of the genera *Ibacus* (e.g., butterfly fan lobster) and *Thenus* (e.g., flathead lobster and *T. indicus*), with a species mean of 19.1 cm TL (SD 6.1) (Stewart et al., 1997; Courtney et al., 2001), compared with L_{50} values for species of the genus *Scyllarides* (e.g., blunt slipper lobster, Galapagos slipper lobster, and hooded slipper lobster), with a species mean of 25.0 cm TL (SD 5.6) (Demartini et al., 2005; Hearn and Toral-Granda, 2007; Oliveira et al., 2008). Oliveira et al. (2008) estimated that the L_{50} for female hooded slipper lobster was 25.1 cm TL—a finding that is very similar to a result of our study (L_{50}=25.3 cm TL).

Oliveira et al. (2008) noted that copulation in the hooded slipper lobster occurs immediately after female molting—an aspect of the reproductive biology of this species that could not be assessed in this study because of the absence of molting or recently molted specimens. The absence of molting specimens in landings is most likely related to their reduced movement and the absence of feeding behavior at this stage (Lavalli and Spanier, 2007). These behaviors would preclude a molting lobster from entering a trap; therefore, fishery samples would not provide accurate copulation data.

This bias was not present in a study by Oliveira et al. (2008), who used data from monthly lobster population surveys conducted during diving expeditions at Santa Catarina Island (in southern Brazil), in June at the beginning of the molting and copulation season. Spanier et al. (1988) observed that the Mediterranean slipper lobster begins these biological processes during the same month in the southeastern Mediterranean,

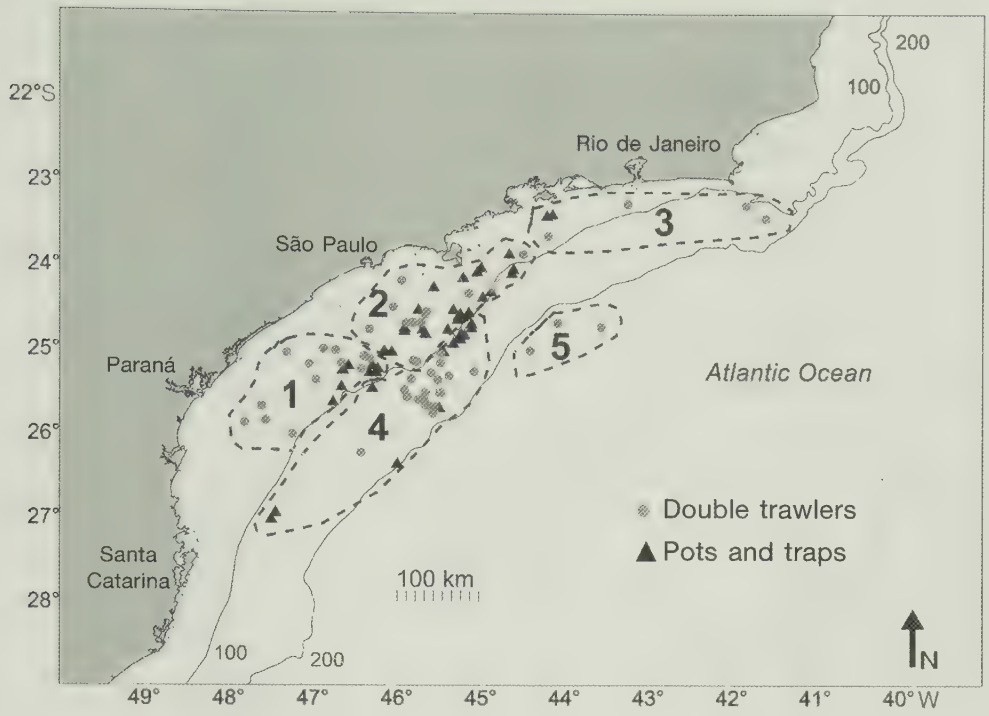

Figure 4

Spatial distribution of sampled effort of the double-trawler and pot-and-trap fleets that caught hooded slipper lobster (*Scyllarides deceptor*) off southeastern Brazil, within the established 5 fishing areas (outlined with dashed lines) from May 2006 through April 2007.

and Lavalli and Spanier (2007) mentioned the rapid calcification of the exoskeleton in species of this family, with the ovigerous condition occurring shortly thereafter. These observations agree with the finding from our study that the relative proportion of ovigerous females of the hooded slipper lobster is greater during August–September than in other periods and with the results of Oliveira et al. (2008).

Another period in our study with a large proportion of ovigerous females occurred during January–February, indicating that there are 2 spawning seasons for the hooded slipper lobster. Lavalli and Spanier (2007) previously reported this spawning period for other *Scyllarides* species. Larvae released in September would experience a period of high primary production in the environment during October–March, when nutrients from the South Atlantic Central Water are present in shallower water (Rossi-Wongtschowski and Madureira, 2006). This reproductive strategy increases the probability of larval survival because complete larval development for *Scyllarides* spp. requires approximately 8 months (Booth et al., 2005).

The range of fecundity values and mean fecundity of hooded slipper lobster in this study were similar to those values reported for other species of the same genus (see review by Oliveira et al., 2008). According to these authors, hooded slipper lobster (n=29) had fecundities between 58,871 and 517,675 eggs (mean=191,262 eggs (SD 17,811).

Research by Vazzoler (1996) suggested that the early maturity of a species lowers fecundity and increases oocyte size to preserve energy per egg and improve larval survival and reproductive success. This reproductive strategy is evident in Scyllaridae, as seen in the relationship between the mean sizes of lobster species and their gonadal maturation, fecundity, and egg diameter. According to Oliveira et al. (2008), the species of *Ibacus* and *Thenus* showed lower fecundity (13,000–21,000 eggs) and larger egg diameters (1.1–1.2 mm) than the fecundity (90,000–224,000 eggs) and egg diameters (0.60–0.67 mm) of species of *Scyllarides*. This observation reflects the reproductive strategy in Scyllaridae, which appears to differ depending on the bathymetric distribution of a given species. Species that are coastal, for example, tend to have lower fecundity and larger egg sizes (e.g., the flathead lobster and butterfly fan lobster, according to Courtney et al. [2001] and Stewart et al. [1997]) than species that inhabit deeper waters (e.g., the blunt slipper lobster, according DeMartini et al. [2005], and the hooded slipper lobster, as observed in this study).

Results from our study indicate that females of the hooded slipper lobster reach a larger size (maximum TL) than males (female: 36.0 cm TL; male: 32.6 cm TL),

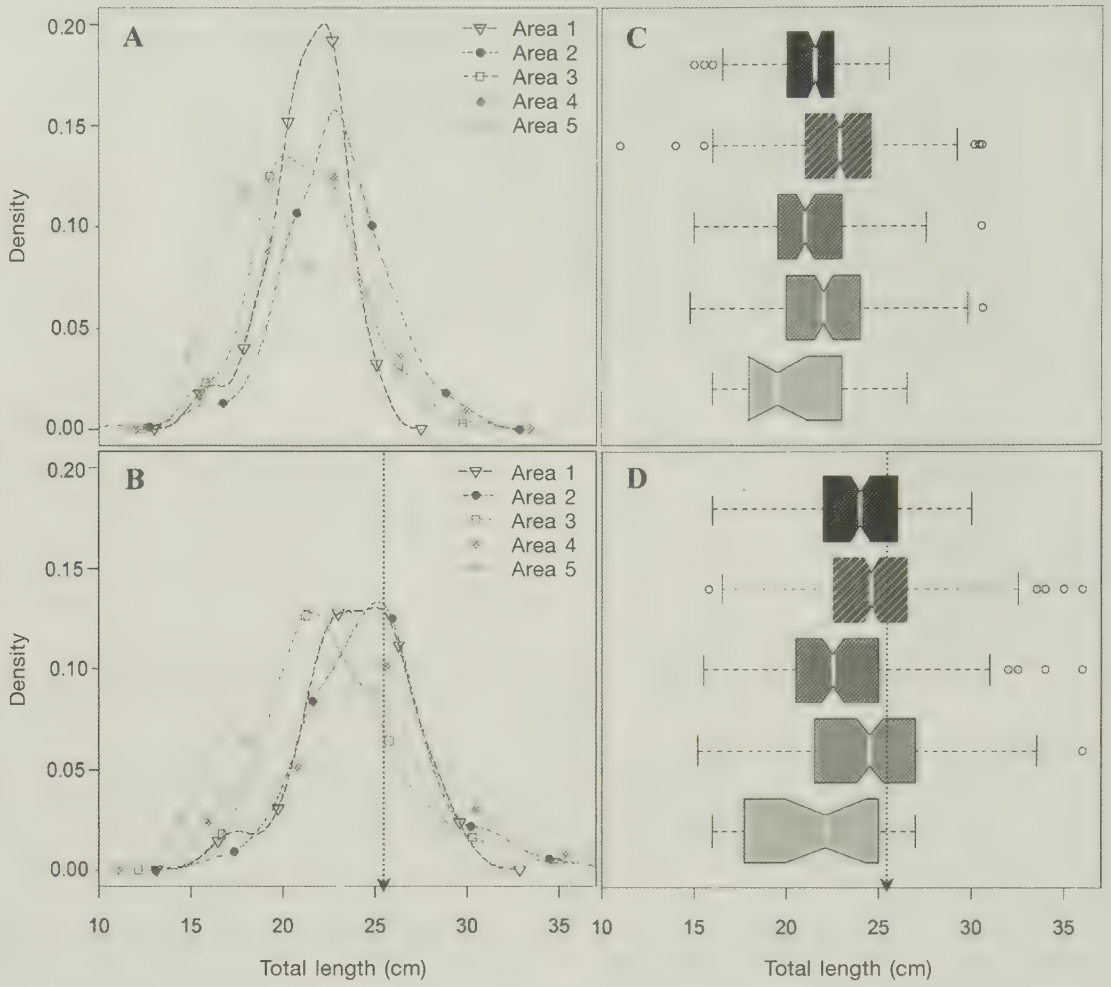

Figure 5

Density curves for different fishing areas for (**A**) males and (**B**) females and medians, quartiles (Q1=lower quartile, cuts off lowest 25% of data and Q3=upper quartile, cuts off highest 75% of data), and ranges for (**C**) males and (**D**) females of the total lengths of the hooded slipper lobster (*Scyllarides deceptor*) caught by pot-and-trap and double-trawler fleets off southeastern Brazil from May 2006 through April 2007. The different shadings for graphics located on the right side: from the darker to lighter (top to bottom) indicate areas in numerical order (1, 2 [dashed lines in white], 3, 4, and 5, respectively). Arrows mark the capture of juvenile and adult females.

in agreement with the results of Oliveira et al. (2008), who observed females that were 36.0 cm TL and males that were 31.0 cm TL. This characteristic is common in the Scyllaridae, but the opposite phenomenon occurs in the Palinuridae and Nephropidae (Spanier and Lavalli, 2007). In our study, the maximum sizes obtained were larger than the 32 cm TL reported by Holthuis (1991) and Spanier and Lavalli (2007). However, the hooded slipper lobster measured in our study were captured farther southeast in Brazil than were the hooded slipper lobster observed by Holthuis (1991) and Spanier and Lavalli (2007), and the lobster in our study were caught at maximum sizes that were similar to those of lobster found south of Brazil by Oliveira et al. (2008).

Those authors also identified 2 migration patterns for the hooded slipper lobster. One of them occurs daily and relates to foraging, and the other is seasonal for the hatching of larvae in shallower water. This latter migration pattern was confirmed in our study because only 4.5% of females were recorded at depths >100 m (area 4), and the remaining females were captured in shallow areas (mean depth <100 m): 27.3%, 63.6%, and 4.5% in areas 1, 2, and 3, respectively. According to information from fishermen in both fleets, each fishing area has the following typical substrate properties (granulometric predominance): area 1=sand, mud, and gravel (calcareous algae); area 2=mud and sand; area 3=sand and gravel; area 4=mud and sand; and

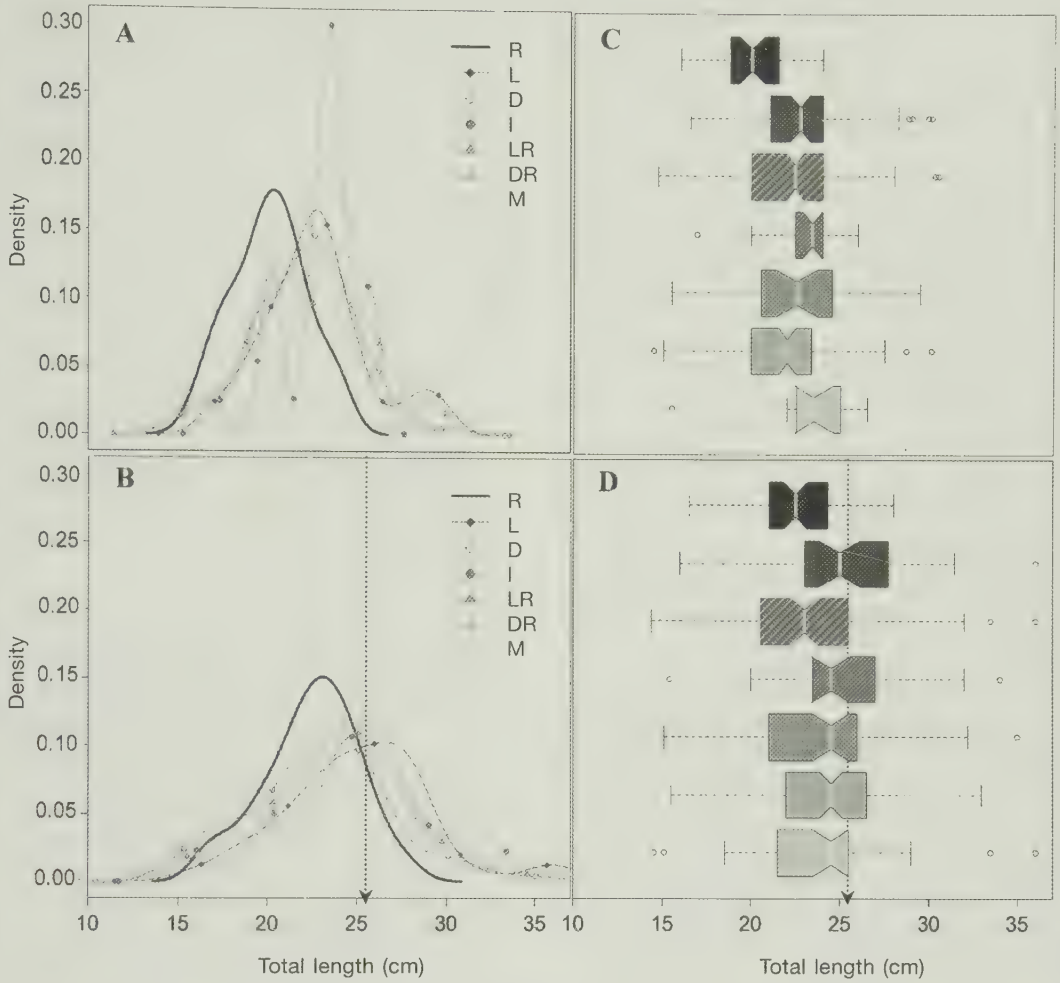

Figure 6

Density curves for the various carapace color patterns, red (R), light (L), dark (D), intermediate (I), light red (LR), dark red (DR), and mixed (M) for (**A**) males and (**B**) females and medians, quartiles (Q1=lower quartile, cuts off lowest 25% of data and Q3=upper quartile, cuts off highest 75% of data), and ranges for (**C**) males and (**D**) females of the total lengths of the hooded slipper lobster (*Scyllarides deceptor*) caught by pot-and-trap or double-trawler fleets off southeastern Brazil from May 2006 through April 2007. The different shadings for graphics located on the right side: from the darker to lighter (top to bottom) indicate various carapace color patterns (R, L, D [diagonal white lines], I, LR, DR, and M, respectively). The arrows mark the capture of juveniles and adult females.

area 5=mud and sand. However, Figueiredo and Tessler (2004) report that the substrate varies greatly in microscale and therefore hampers association analyses.

In decapod crustaceans, carapace color patterns are a result of hormonal control of chromatotropines (Rao, 1985), combined with external factors, such as food sources, substrate color, and seasonal and environmental variations (Rao, 1985; Bedini, 2002). These patterns may also be associated with intrinsic biological factors, such as growth, reproduction, mating, and sexual maturation during ontogeny (Ryan, 1967; Pinheiro and Taddei, 2000). Analysis of the carapace color patterns of the hooded slipper lobster in this study did not help to identify the reproductive period, timing of molting, or fishing areas for this lobster.

Chromatic changes during the ontogeny of crustaceans have been reported by Abele (1982) and Dalabona et al. (2005), particularly changes associated with maturation, as observed for other decapods of the genera *Callinectes* (Baldwin and Johnsen, 2012) and *Arenaeus* (Pinheiro and Taddei, 2000). In this study, there was a relationship between the size (TL) of females with red carapaces (range: 16.5–29.0 cm TL; mean; 22.7 cm TL [SD 2.9]) and L_{50} (25.3 cm TL), a size that was very

similar to the smallest ovigerous female registered in this study (22.5 cm TL). Therefore, it may be that the red chromatic pattern is related to maturation changes for this species, and this relationship should be evaluated in future experiments. The other coloration patterns were observed in lobster with a great range in size (TL) and were common to both sexes, possibly because color changes are more related to the time since molting, microscale substrate type, and trophic ecology of this species. There is a lack of specific studies concerning these influences, however.

For species of Scyllaridae, males are smaller than females (Lavalli and Spanier, 2007; Oliveira et al., 2008) and become mature at smaller sizes (e.g., *Ibacus* spp., according to Stewart et al., 1997). It is possible that red coloration may be used as an indicator of the chromatic changes in maturing males because the size distribution for this coloration was restricted to the range of 16.0 to 25.5 cm TL, with a mean of 20.4 cm TL (SD 2.7). On the basis of these results, it is likely that the L_{50} for males was approximately 23 cm TL, although more detailed analyses are required to confirm this hypothesis.

The reduction in stock sizes of hooded slipper lobster in our study area (see Duarte et al., 2010) presumably was enhanced by the capture of immature females (66.9%) with the 2 fishing methods: 1) trawlers and 2) pots and traps. On the basis of that observation, our research results indicate that the following potential measures could be investigated for the hooded slipper lobster fisheries in southeastern Brazil:1) the use of a minimum landing size of 25 cm TL for this species, regardless of sex, and the release of individuals smaller than this size; 2) the release of ovigerous females immediately after capture to prevent an effect on recruitment; and 3) a closed season for fisheries from August to September, when there is the greatest reproductive activity (proportion of ovigerous females) for this species.

However, because discard mortality can be high in spiny lobsters (Gooding, 1985; O'Malley, 2008), whether discarding of hooded slipper lobster would be effective for stock protection is uncertain. Nevertheless, Castro et al. (2003) demonstrated the efficacy of releasing caught fish of the genus *Nephrops* as a management measure. Haddy et al. (2005) and Spanier and Lavalli (2006) suggested that slipper lobsters are more resistant to discard mortality, because of their thicker carapace (Melo, 1999), and usually return alive to the water. In addition, management actions, such as size limits, release of ovigerous females, and closed seasons were effective management controls for the *Panulirus cygnus* fishery (Hall and Chubb, 2001), indicating that such measures could be pertinent for slipper lobster fisheries.

In this study, we examined the life history aspects of the hooded slipper lobster landed as bycatch in 2 fisheries in Brazil. The biometry, reproductive status, and size structure were documented. Our main findings were that maturity was related to the sizes of abdomen (females) and carapace (males); the ovigerous specimens occurred mainly in shallow waters, where fisheries were more intense; and higher numbers of juveniles than of adults were reported by fishing fleets with landings in the study area. In addition, it is possible that the red color of the carapace was related to maturation changes for this species. These results agree with evidence of fishing pressure on the slipper lobster population that was documented in other studies (Lavalli and Spanier, 2007; Spanier and Lavalli, 2007; Duarte et al., 2010).

Nevertheless, further studies are clearly still necessary, especially those that examine the life cycle and other parameters of the current populations of slipper lobsters in Brazil to understand mortality, growth, recruitment, stock identities, and stock levels of the hooded slipper lobster in waters of southeastern Brazil.

Acknowledgments

We thank all of the captains, fishermen, and dock workers at the various landings who contributed to this study. We also recognize the Instituto de Pesca (Santos, São Paulo), its Graduate Program in Fisheries and Aquaculture, and several colleagues for their input and help. We acknowledge the advice and help received from several colleagues, especially G. Pinheiro, who gave special attention to the figures in our manuscript. M. Pinheiro and M. Gasalla are grateful to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the research fellowships provided. We also thank the reviewers who contributed much to improve this study.

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Modeling the growth of recruits of European hake (*Merluccius merluccius*) in the northwestern Mediterranean Sea with generalized additive models

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Abstract—In this study, the growth pattern of juvenile European hake (*Merluccius merluccius*) was analyzed in relation to oceanographic and ecological factors in the Ligurian Sea and northern Tyrrhenian Sea, both part of the Mediterranean Sea. The ages of juvenile European hake, collected during a trawl survey in June 2011, were estimated by reading otolith daily growth rings. The growth pattern (length–age relationship) of juvenile European hake recruited to the population (<1 year old) was analyzed by fitting a multivariate generalized additive model with explanatory variables: depth, bottom temperature, sea-surface temperature, scalar wind speed, chlorophyll-*a* concentration, and fish density (number of individuals per square kilometer). A significant effect of density on the length–age relationship was found, and an increased growth rate at densities >3000 individuals km^{-2}. This observed positive effect of density on growth could be argued to be a consequence of favorable environmental conditions, such as food availability and temperature, where both fish density and growth are maximized. Conversely, areas of lower density correspond to habitats of low suitability, where growth is impaired.

Manuscript submitted 10 August 2013.
Manuscript accepted 3 December 2014.
Fish. Bull. 113:69–81 (2015).
doi: 10.7755/FB.113.1.7

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The European hake (*Merluccius merluccius*) is a demersal fish widely distributed in the Mediterranean Sea and in the northeastern Atlantic (Murua, 2010). In the Mediterranean Sea, it is a major component of the demersal fish assemblages on both the continental shelf and the upper slope (Orsi Relini et al., 2002; Colloca et al., 2004). Juvenile European hake aggregate in nursery areas located on the continental shelf break (Maynou et al., 2003; Abella et al., 2005; Bartolino et al., 2008a; Hidalgo et al., 2008), and adult fish can be found in a wider depth range from the shelf to the upper slope (Aldebert et al., 1993; Sbrana et al., 2007; Cartes et al., 2009; Bartolino et al., 2011). Because of its abundance and wide spatial distribution, the European hake is one of the most highly exploited species in the Mediterranean Sea, targeted by multigear fisheries. The bulk of the catch of this species is obtained from trawl fisheries, which mainly exploit the youngest portion of the population (≤30 cm in total length [TL]). However, there are still relatively high discard rates of undersize fish (Cardinale et al., 2011) despite an amendment in 2010 in the European Union Council Regulation to increase trawl codend mesh size (European Union Council Regulation 1967/2006). The adult fraction (>40 cm TL) is exploited by gillnet and longline fisheries (Sbrana

et al., 2007; Bartolino et al., 2011). This pattern results in high exploitation rates across the entire population, from small individuals (<15 cm TL) to large females (>60 cm TL) in spawning aggregations (Aldebert et al., 1993) and highlights the importance of management measures to reduce the catch of both juveniles and spawning adults (Drouineau et al., 2010).

The very high concentration of juvenile European hake along the coasts of Italy in the Ligurian and Tyrrhenian Seas indicates that these areas are the main European hake nurseries in the northwestern Mediterranean basin (Orsi Relini et al., 2002; Colloca et al., 2009). Orsi Relini et al. (2002) estimated mean densities of European hake recruits to be up to 8 times higher than densities reported for other nurseries in the Mediterranean Sea. In the Tyrrhenian Sea, at the boundary between the continental shelf and the upper slope, densities >25,000 individuals km^{-2} have been observed (Colloca et al., 2009).

Despite many studies of the biology of European hake in the Mediterranean Sea, the growth pattern of juveniles is still controversial (Drouineau et al., 2010). It is not clear whether the reported variability in the growth rate of European hake juveniles is due to methodological differences in the approaches used for age determination or due to natural variability in growth processes.

Atmospheric processes and oceanographic features are known to have a key role in recruit condition and recruitment strength of other fishes. A link between environmental variables (e.g., climate variability, temperature, and phytoplankton production) and recruitment of Atlantic cod (*Gadus morhua*) in the North Sea and northeastern Atlantic has been described previously (Köster et al., 2005; Steingrund and Gaard, 2005; Stige et al., 2006; Beggs et al., 2014). Furthermore, increases in temperature in the North Sea have been reported to affect growth dynamics of haddock (*Melanogrammus aeglefinus*) (Baudron et al., 2011). Thermal conditions have been reported to affect recruitment and distribution of Pacific cod (*Gadus macrocephalus*) in the eastern Barents Sea (Hurst et al., 2012), of Pacific hake (*Merluccius productus*) along the western coast of North America (Agostini et al., 2008), and of Chilean hake (*Merluccius gayi gayi*) in the south Pacific (San Martín et al., 2013). Within-year variability in growth of recruits of Argentine hake (*Merluccius hubbsi*) in response to environmental variables was found by Norbis et al. (1999) along Uruguayan coasts, and interannual variability in growth was found in Pacific hake (Woodbury et al., 1995).

Density-related growth relationships also have been described for a range of species: Bromley (1989) found a negative relationship between growth and fish density in both 1-year-old (I group) and 2-year-old (II group) Atlantic cod, whiting (*Merlangius merlangus*), and haddock in the North Sea: fish in areas of low density were larger than fish in areas of high density, possibly because of feeding competition in high density areas. Although environmental and oceanographic features are known to affect recruit condition and recruitment strength of European hake (Alvarez et al., 2001; Maynou et al., 2003; Olivar et al., 2003; Abella et al., 2008; Bartolino et al., 2008a; Hidalgo et al., 2008), understanding of the effect of those factors on the growth dynamics of juvenile European hake is still limited.

The aim of the present study was to model the growth of European hake juveniles to determine the effects of environmental variables (i.e., sea-surface temperature, bottom temperature, depth, scalar wind speed, chlorophyll-*a*) and population factors (i.e., fish density) using a generalized additive model (GAM) (Hastie and Tibshirani, 1990).

Materials and methods

Study area

For this study, the growth pattern of juvenile European hake was analyzed in northwestern Italian waters, which include the Ligurian Sea and the northern Tyrrhenian Sea (Fig. 1). The Tyrrhenian Sea is generally considered a distinct entity within the western Mediterranean basin because it is semi-enclosed between the islands of Corsica, Sardinia, and Elba and the mainland (Italy) and is separated from the rest of the western basin by a channel of moderate depth, about 1500 m (Orfila et al., 2005). Along the central western Italian coasts, the Tyrrhenian Current, also called the Eastern Corsica Current, flows northward through the Corsica Channel into the Ligurian Sea. The Corsica Channel is the passage between the islands of Corsica and Elba that connects the northern Tyrrhenian Sea to the southern Ligurian Sea. It plays a key role for water circulation in the northwestern Mediterranean Sea because the water exchange that runs through it involves the whole water column (Gasparini et al., 1999).

The general seasonal pattern of phytoplankton dynamics is typical of subtropical areas, with a bloom period of maximum productivity from February to April and a period of minimum productivity in summer months. The intensity of this winter–spring bloom varies significantly between years. In the Ligurian Sea, a substantial positive correlation links the intensity of the phytoplankton winter–spring bloom with a strong autumn–winter water turbulence (which is mainly driven by winds), and reduced wind mixing in March (Nezlin et al., 2004).

Trawl sampling and environmental data

Specimens of juvenile European hake were collected from 13 of the 120 trawl stations sampled in June 2011 during an experimental bottom trawl survey, the Mediterranean International Trawl Survey (MEDITS; see Bertrand et al., 2002, for technical specifications) in the Ligurian and northern Tyrrhenian Seas (Fig. 1). To

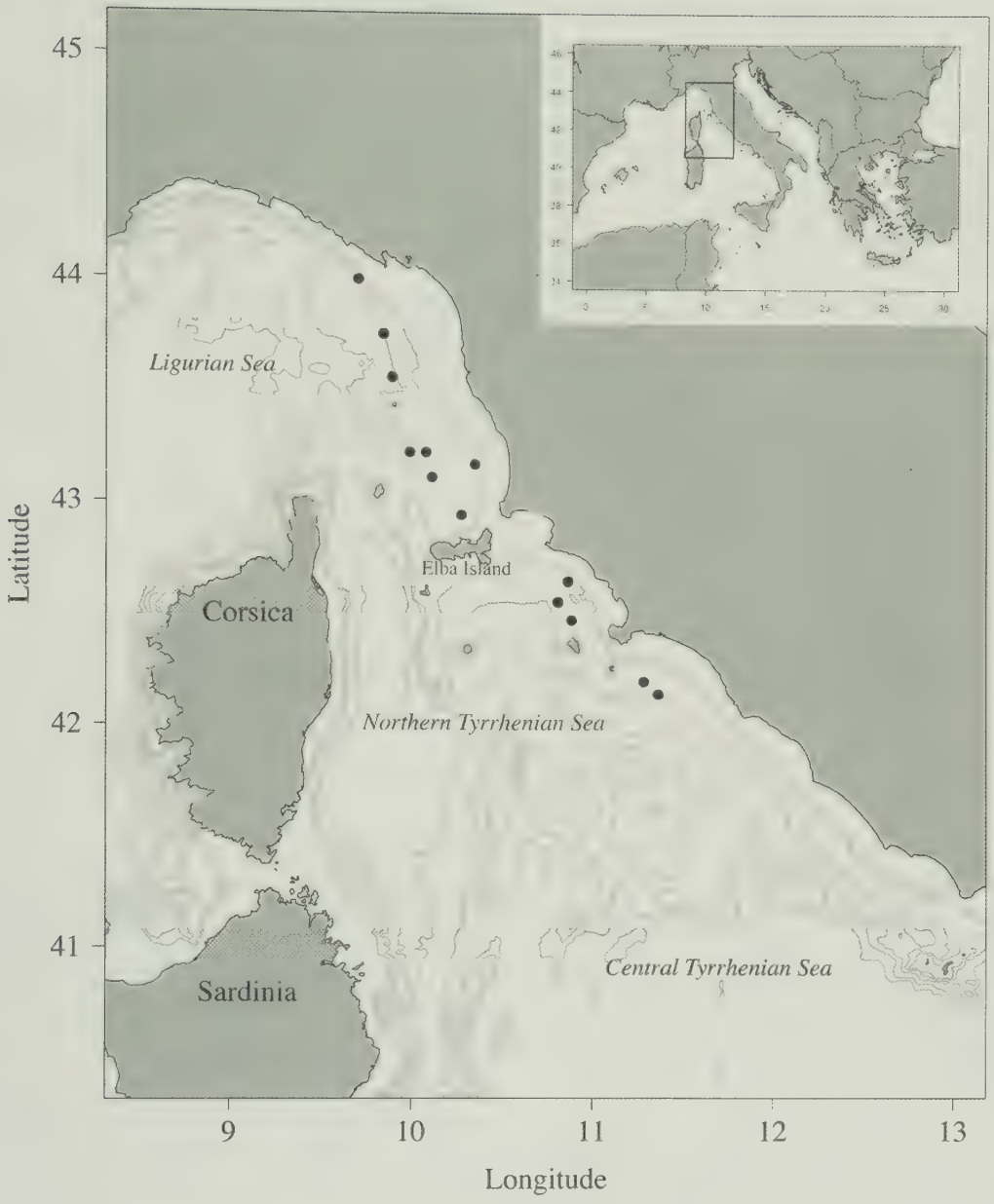

Figure 1

Map of the study area in the Ligurian Sea and northern Tyrrhenian Sea. Black circles indicate the 13 sites where European hake (*Merluccius merluccius*) were sampled in June 2011 during the Mediterranean International [bottom] Trawl Survey (MEDITS). Gray lines show the 100-, 200-, 500-, 1000- and 1500-m isobaths.

cover the relevant nursery areas, identified by Colloca et al. (2009), 5 of the 13 stations from which specimens were collected were located in the Tyrrhenian basin and 8 were located in the Ligurian Sea.

For each station, a suite of oceanographic and ecological variables that potentially affect growth processes of the European hake was obtained (Table 1). Satellite data at a fine spatial scale for sea-surface temperature (SST, degrees Celsius), scalar wind speed (meters per second), and chlorophyll-*a* concentration (milligrams per cubic meter) were used (MyOcean follow-on project, http://www.myocean.eu); daily data were averaged for the period of January–March 2011. Bottom temperature (degrees Celsius) was measured and mean depth (meters) was recorded at each station by using a DST centi-TD[1] temperature and depth probe, with

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1

Environmental and ecological variables used in the generalized additive model (GAM) of environmental effects on growth of juvenile European hake (*Merluccius merluccius*) in the northwestern Mediterranean Sea. European hake were sampled in June 2011 in the Tyrrhenian Sea (Tyr) and Ligurian Sea (Lig). Latitude (Lat.) and longitude (Long.) of the mean point of each haul are shown, as well as the number of specimens (otoliths), mean bottom temperature (Bottom temp.), mean depth, and recruit density (number of individuals per square kilometer) recorded in each haul, the mean sea-surface temperature (SST), mean wind scalar speed, and mean concentration of chlorophyll-*a* (chl-*a*) used in the GAM.

Haul code	Area	Lat.	Long.	Number of otoliths	Bottom temp. (°C)	Mean depth (m)	Recruit density (individuals km^{-2})	SST (°C)	Mean scalar wind speed ($m\ s^{-1}$)	Chl-*a* ($mg\ m^{-3}$)
42	Tyr	4208.07	1121.43	14	13.9	156	3214.0	14.00	6.53	0.449
43	Tyr	4211.32	1116.55	22	14.0	124	3571.0	14.00	6.53	0.443
59	Tyr	4227.59	1052.53	24	13.9	131	8319.0	13.80	6.31	0.438
62	Tyr	4237.86	1051.43	22	13.9	109	6631.0	13.87	6.31	0.413
63	Tyr	4232.51	1047.81	23	13.8	164	7377.0	13.83	6.31	0.424
91	Lig	4255.79	1015.80	21	13.7	113	1008.0	13.87	5.57	0.457
94	Lig	4313.11	958.73	21	13.6	251	3159.0	13.50	7.74	0.448
98	Lig	4332.80	952.79	19	13.5	241	6835.0	13.42	7.74	0.441
100	Lig	4312.68	1003.93	20	13.6	153	1819.0	13.63	7.74	0.408
103	Lig	4306.27	1006.32	28	13.6	150	1378.0	13.62	7.74	0.426
115	Lig	4344.53	950.26	18	13.4	205	3197.0	13.42	8.54	0.449
126	Lig	4309.57	1020.49	22	13.8	101	1072.0	13.59	7.74	0.434
131	Lig	4359.29	941.66	17	13.4	140	2003.0	13.48	8.54	0.414

supporting SeaStar software (Star-Oddi, Gardabaer, Iceland), attached to the trawl net. European hake juveniles were identified according to the morphological features described by Murua (2010). At each station, density (number of individuals per square kilometer) of juvenile European hake was computed as the ratio between the number of recruits and the swept area (unit of measurement km^2).

Otolith reading

All specimens of European hake that were caught at the 13 selected stations were measured in TL to the nearest 0.5 cm; otoliths (sagittae) were removed from a subsample of 318 individuals that ranged in size from 4.5 to 18.0 cm TL. The upper size limit of 18.0 cm TL was used to define European hake recruits (fish in their first year of life) (Belcari et al., 2006). The length-frequency distribution of the specimens caught at the 13 stations was broken down into normal components by using Batthacharya's method (Bhattacharya, 1967).

Left sagittae were ground on wet sandpaper, polished on abrasive cloth with alumina slurry, and mounted external-side up on glass slides with a 2-component epoxy resin; a second grinding and polishing procedure was performed to obtain thin frontal sections (Belcari et al., 2006). Microstructure analysis (counting of daily growth rings) of otolith sections was carried out with a compound green-light, polarizing microscope with plan apochromatic objectives. The number of daily increments deposited within the primordium, the central area of the otolith (Morales-Nin and Moranta, 2004), was recorded to estimate the duration of the presettlement period of this species (Arneri and Morales-Nin, 2000; Morales-Nin and Moranta, 2004; Belcari et al., 2006).

Otolith readings were used to back-calculate the hatching-date distribution by subtracting the fish age from the date of capture. An indirect validation of the periodicity of increment formation was obtained by comparing the estimated hatching-date distribution with the spawning period of the species (Arneri and Morales-Nin, 2000; Panfili et al., 2002; Belcari et al., 2006). To estimate the age-frequency distribution and to back-calculate the hatching-date distribution, the age-length key that resulted from the readings was applied to the length-frequency distribution that was obtained from the 13 stations that were sampled. In addition, a subsample of 40 otoliths was reread by the same operators for evaluation of the match between the readings (Belcari et al., 2006).

Data analysis

A multivariate GAM with Gaussian distribution was used to describe the growth of juvenile European hake, specifically the length–age relationship and environmental covariates. For the initial model that was used

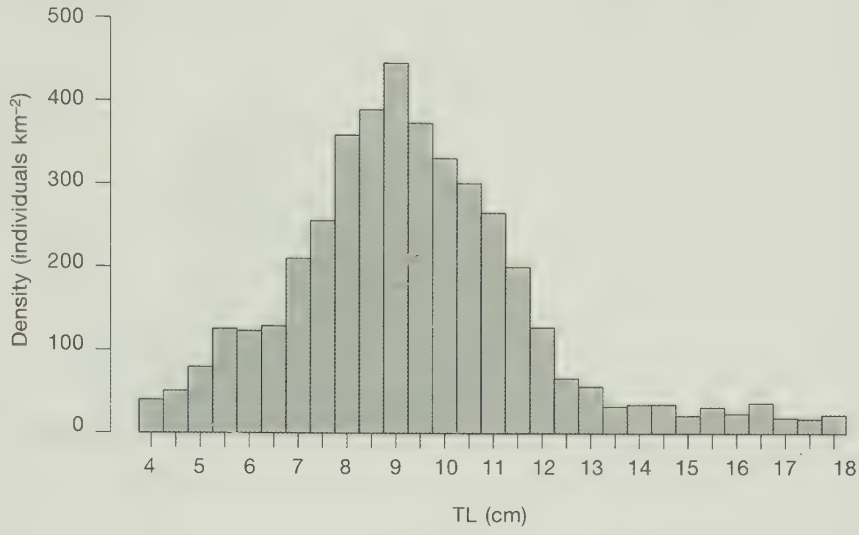

Figure 2

Length-frequency distribution of European hake (*Merluccius merluccius*) obtained from 13 stations sampled in the Ligurian Sea and northern Tyrrhenian Sea in June 2011 during the Mediterranean International [bottom] Trawl Survey (MEDITS). Lengths for fish ≤18 cm in total length (TL) are shown in size classes of 0.5 cm TL.

to define the length–age relationship with covariates, the following equation was used:

$$Length = \alpha + f_1(Age) + f_2(bottom\ T) + f_3(density) + f_4(depth) + f_5(SST) + f_6(wind) + f_7(\text{chl-}a) + f_8(depth{:}density) + factor(Area) + \varepsilon_i, \quad (1)$$

where bottom T, density, and depth = the bottom temperature, European hake recruit density, and depth from each station, respectively; and *SST*, *wind*, and chl-*a* = sea-surface temperature, scalar wind speed and chlorophyll-*a* concentration averaged over the period of January–March 2011.

To evaluate possible differences in recruit growth patterns, the area (Ligurian Sea or Tyrrhenian Sea) was included in the analysis and treated as a factor (*Area*). Following the findings by Bartolino et al. (2008b), which included observation of a stable pattern of depth preference by juvenile European hake, the interaction between depth and fish density (f_8) was also included in the GAM.

Two forms of this model were constructed. With the first, a continuous variable of density was assumed; this first form was compared with a second model in which density was treated as a 3-level factor: low (<2000 individuals km^{-2}), medium (2000–4000 individuals km^{-2}) and high (>4000 individuals km^{-2}). Then, the fit of these models was compared. Analysis of variance was used to test for a significant difference in model fit, and the model with the lowest Akaike's information criterion (AIC) was selected as the best model, which is the model that best fits the set of data.

The degree of collinearity between explanatory variables was tested with plots of paired variables (pairplots), a matrix of scatter plots that show the bivariate relationships of variables, and variance inflation factor (VIF) values (Zuur et al., 2009). Variables with a high Pearson's correlation coefficient (r) (>0.8, absolute value) and a high VIF value (>3) were considered correlated, and one of the pair was removed. A backward stepwise model selection procedure based on analysis of variance and on the AIC was used to identify the most parsimonious model with the greatest explanatory power. The significance of each variable in the GAM was determined by means of analysis of variance (F-test). The levels of constraints (k) for splines were reduced from a maximum, but still achieving convergence to 1. The level of constraint for the number of splines that were used in the final analysis was selected by a comparison of AIC scores. Model residuals were tested for assumptions of homogeneity and normality (Zuur et al., 2009). A multiple linear regression model that used the final selected explanatory variables also was compared with the GAM model by using analysis of variance and AIC. Data exploration and analyses were carried out with the package R, vers. 2.15.2, and the associated mgcv package (R Core Team, 2012). An assumed significance level of 5% was used in all statistical analyses.

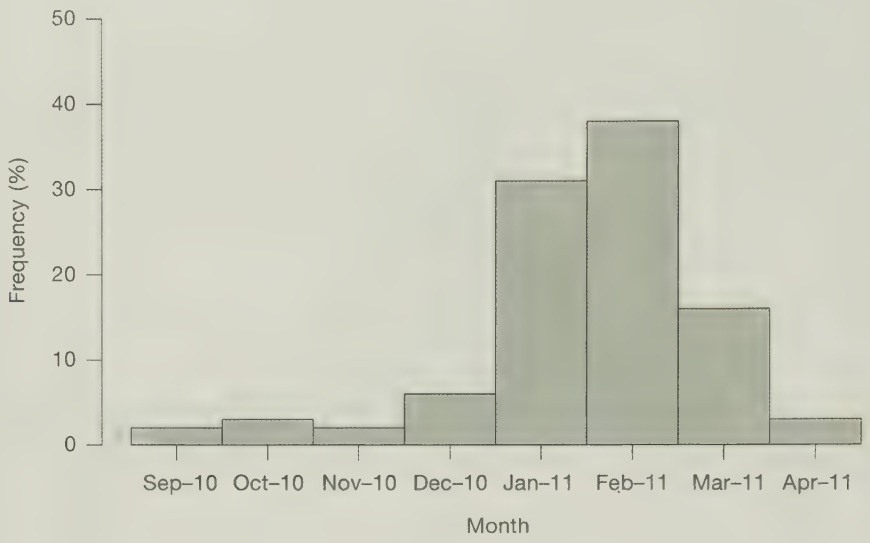

Figure 3

Distribution of back-calculated hatching dates for recruits of European hake (*Merluccius merluccius*) caught in June 2011 during the Mediterranean International [bottom] Trawl Survey (MEDITS) in the Ligurian Sea and northern Tyrrhenian Sea.

Results

At the 13 selected stations, 3123 specimens of European hake were caught during the 2011 MEDITS in the Ligurian Sea and northern Tyrrhenian Sea. Sizes ranged from 4.0 to 41.0 cm TL; the length-frequency distribution of the specimens belonging to the first year class (up to 18 cm TL) is shown in Figure 2. The length-frequency distribution showed a single normal component with mean size of 9.0 cm TL (standard deviation [SD] 2.0).

Counts of otolith daily increments from microstructure analysis ranged from 77 to 340. The number of increments within the primordium of the otolith ranged between 36 and 70, with an average of 50 (SD 5). The results of the rereading of 40 otolith slides used by Belcari et al. (2006) showed no discrepancies larger than 10%, a proportion that is considered a reading precision threshold (Arneri and Morales-Nin, 2000), providing further support for the reading method used in the present study.

Back-calculation of hatching dates provided estimates of the main hatching period to be from December 2010 to March 2011, with a peak during January–February 2011 (Fig. 3).

A subsample of 271 individuals was used to fit the growth model by means of GAM. The 271 individuals were born during the main hatching period (December 2010–March 2011) with a size range between 4.5 and 13 cm TL and an age range between 77 and 205 days (Fig. 4); therefore, they represented a single cohort.

Data exploration highlighted collinearity between area, bottom temperature, SST, and scalar wind speed (Fig. 5), supported by r >0.8 and VIF values >3. Therefore, area, SST, and scalar wind speed were removed from the model, and a model containing age, bottom temperature, fish density, depth, chlorophyll-*a*, and the second-order interaction depth:density as explanatory variables was tested by means of analysis of variance and backward selection:

$$Length = \alpha + f_1(Age) + f_2(bottom\ T) + f_3(density) + f_4(depth) + f_5(\text{chl-}a) + f_6(depth{:}density) + \varepsilon_i. \quad (2)$$

Based on backward selection, the best model (Table 2), with variables significant only at the 5% level and with the lowest AIC (689.3), contained only age and density as explanatory variables:

$$Length = \alpha + f_1(Age) + f_2(density) + \varepsilon_i. \quad (3)$$

That final model explained 81% of the total deviance, with a generalized cross-validation score of 0.727. The multiple linear regression model fitted with the same explanatory variables had heterogeneity within the model residuals, as well as a higher AIC (704.2). The analysis of variance between these models was significant (F=9.221, P<0.05), indicating that the smoothers were not linear.

The explanatory variable *age* had a linear effect, although with some fluctuations, especially in the first

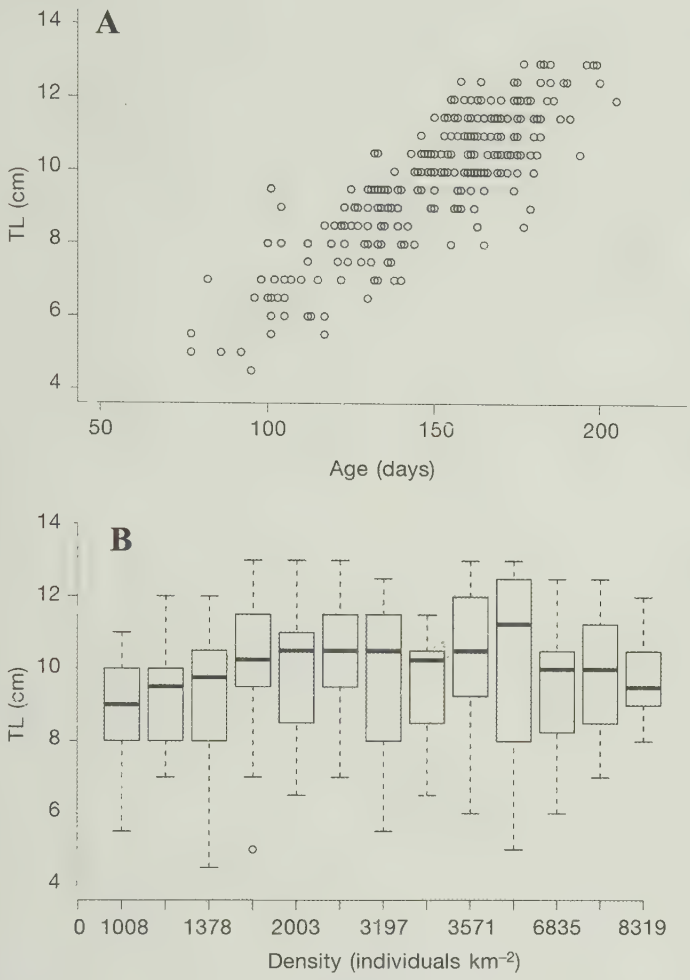

Figure 4

For the subsample of 271 European hake (*Merluccius merluccius*) recruits caught in June 2011 during the Mediterranean International [bottom] Trawl Survey (MEDITS) in the Ligurian Sea and northern Tyrrhenian Sea, (**A**) length-at-age data distribution and (**B**) a boxplot of length data conditional on density.

part of the age range. However, in the older part of the age range, the smoothing function that describes the relationship between age and length flattened, indicating a decrease in growth rate. The effect of density on the growth rate was positive up to 3000 individuals km^{-2}, and had a weak negative effect at higher densities (Fig. 6). At the stations that had a recruit density higher than 3000 individuals km^{-2}, the length at age was on average 0.5 cm TL greater than the length at age observed at stations with lower densities.

The value of k selected for the final analysis of the effect of density, by comparison of AIC scores, was 4. The AIC was higher when values of k >4 were used, and a "dome-shaped" effect caused by the lack of observations of densities between 3700 and 6000 individuals km^{-2} was evident. With k set at a value of 4, the effect of density showed an increasing trend up to 3700 individuals km^{-2} and then a rather constant pattern at higher densities, limiting the effect caused by fitting the model in the area where values of density were missing in the database. Further, the use of the variable density as a factor (3-level factor) was tested. The results were similar to those obtained with the model that had a continuous variable of density: increasing growth rate with density, although with a slight decrease at very high densities. However, this model had a higher AIC and, therefore, was less suitable in its fit to the data than the model that used density as a continuous variable and a k value of 4. An inspection of the graphs for the model (Fig. 7) shows that there was no evidence of a pattern within the model residuals.

Discussion

Despite the ongoing debate about general issues of age estimation in European hake, reading daily growth rings on otoliths has proved to be a useful tool in the understanding of the first year of growth (Arneri and Morales-Nin, 2000). The use of annual rings on otoliths led to the assumption that the European hake grows slowly (Drouineau et al., 2010), but further studies on adult growth that have used tagging campaigns (de Pontual et al., 2003; Piñeiro et al., 2007) and analysis of otolith daily increments in juveniles (Arneri and Morales-Nin, 2000; Morales-Nin and Moranta, 2004; Kacher and Amara, 2005, Belcari et al., 2006; Piñeiro et al., 2008; Otxotorena et al., 2010) have revealed that the growth rate is probably much faster than previously thought.

Results from the present study are consistent with the main findings of recent studies on juvenile European hake growth in both the Atlantic and the Mediterranean Sea, which indicate a fast growth rate of about 0.6 mm day^{-1} during the first year of life (Morales-Nin and Moranta, 2004; Kacher and Amara, 2005; Belcari et al., 2006; Otxotorena et al., 2010). Also, the results of back-calculations of birth dates are in agreement with the available knowledge on spawning and recruitment of European hake in the western Mediterranean Sea (Maynou et al., 2003; Abella et al., 2005; Belcari et al., 2006; Recasens et al., 2008).

The present study is one of the first attempts to fit a recruit growth model for European hake with factors that could potentially affect growth dynamics. Through the application of a GAM on the length–age relationship, recruit density (number of individuals per square kilometer) was found to have a significant effect on the growth dynamics of European hake recruits; however,

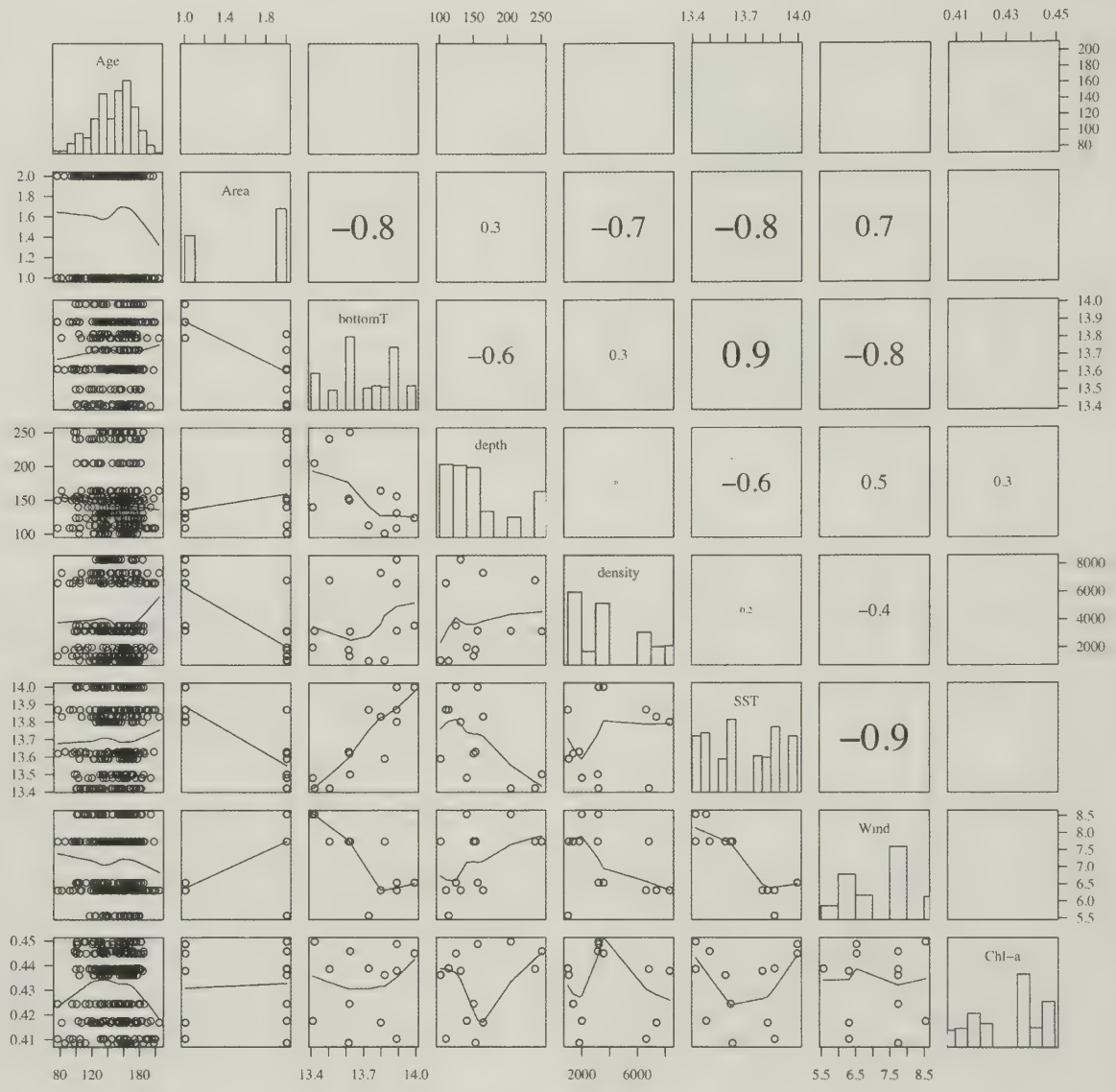

Figure 5

Pairs plot for all the explanatory variables in the data set used for this study of (*Merluccius merluccius*) in the northwestern Mediterranean Sea. The upper diagonal panel shows the Pearson's correlation coefficient, and the lower diagonal panel shows the scatterplots with a smoother added to visualize the pattern. The font size of the correlation coefficient is proportional to its estimated value.

no evidence of effects exerted by oceanographic features were found. Atmospheric processes and oceanographic features instead played a role in determining variations in recruitment strength of European hake (Alvarez et al., 2001; Maynou et al., 2003; Olivar et al., 2003; Abella et al., 2008; Bartolino et al., 2008a). Also, although Hidalgo et al. (2008) found spatial and temporal differences related to environmental and hydrographical variables in recruitment processes and condition of European hake around Balearic Islands, they did not observe any differences in growth of this species.

The observed positive effect of recruit density could be interpreted as an optimal density window where growth is maximized. Fast growth was observed for densities of around 3000 individuals km^{-2}, and growth remained slightly constant at higher densities. Still, recruit growth remained greater in areas of high density of recruits than in areas with low density, which could correspond to habitats of low suitability, where

Table 2

Summary of the backward selection of the best model in the generalized additive model. The best model, with smoothers that are all significant and that has the lowest AIC value, is highlighted in bold. Explanatory variables included mean bottom temperature (temp.); mean depth; recruit density (number of individuals per square kilometer); mean concentration of chlorophyll-*a* (chl-*a*); and age (days). Depth:density is the interaction; "y" and "n" indicate the explanatory variables included and excluded in GAMs. Measures of model fitness were deviance explained (Dev. expl.), coefficient of determination (r^2), generalized cross-validation score (GCV), and Akaike's information criterion (AIC); ns=not significant: $P>0.05$; **=$P<0.01$; ***=$P<0.001$.

Mean bottom temp.	Mean depth	Chl-*a*	Recruit density	Age	Depth: density	Dev. expl. (%)	r^2	GCV	AIC
y^{ns}	y^{ns}	y^{ns}	y**	y***	y^{ns}	80.7	0.795	0.731	692.4
y^{ns}	y^{ns}	y^{ns}	y**	y***	n	80.7	0.794	0.734	691.1
n	y^{ns}	y^{ns}	y**	y***	n	80.6	0.794	0.737	692.3
n	n	y^{ns}	y***	y***	n	80.6	0.795	0.728	690.1
n	**n**	**n**	**y***	**y***	**n**	**80.7**	**0.795**	**0.727**	**689.3**

growth is impaired. Bromley (1989) found a negative relationship between density and growth in some gadoid (Atlantic cod, whiting, and haddock) juveniles in the North Sea.

The ecological factors that affect differences in growth between areas deserve further multiyear investigations, for example, through sampling to examine the abundance of prey, such as macrozooplankton, in the main nursery areas (Ferraton et al., 2007; Cartes et al., 2009). Indirect evidence of the environmental quality of European hake nurseries in the Mediterranean Sea has been inferred from their high spatiotemporal stability (Fiorentino et al., 2003; Colloca et al., 2009). In the Ligurian Sea and Tyrrhenian Sea, after 2 months spent in the pelagic environment (in the present study; also, see Belcari et al., 2006), European hake larvae were transported by eddies and frontal systems to areas of relatively high planktonic production that resulted from upwelling (Abella et al., 2008). These areas are located along the shelf break (Colloca et al., 2004), where production is enhanced by upwelling and water turbulence, both of which increase the transport and nutrient input of organic matter into the water column (Pinazo et al., 1996). The entire trophic chain, therefore, is increased, including a positive effect on the main prey of European hake recruits, in particular euphausiids and mysids, which reach their highest diurnal abundance on the shelf break (Colloca et al., 2004).

The high spatial stability over time of the main hake nurseries in the Ligurian and Tyrrhenian Seas

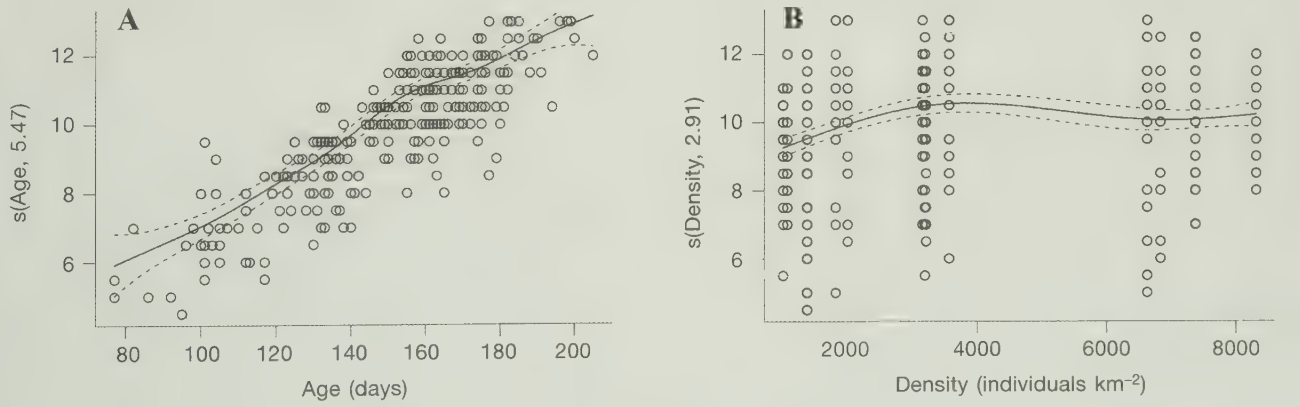

Figure 6

Estimated smoothing curves for the optimal generalized additive model representing the effects of (**A**) age (days) and (**B**) recruit density (number of individuals per square kilometer) on European hake (*Merluccius merluccius*) recruits caught in June 2011 during the Mediterranean International [bottom] Trawl Survey (MEDITS) in the Ligurian Sea and northern Tyrrhenian Sea.

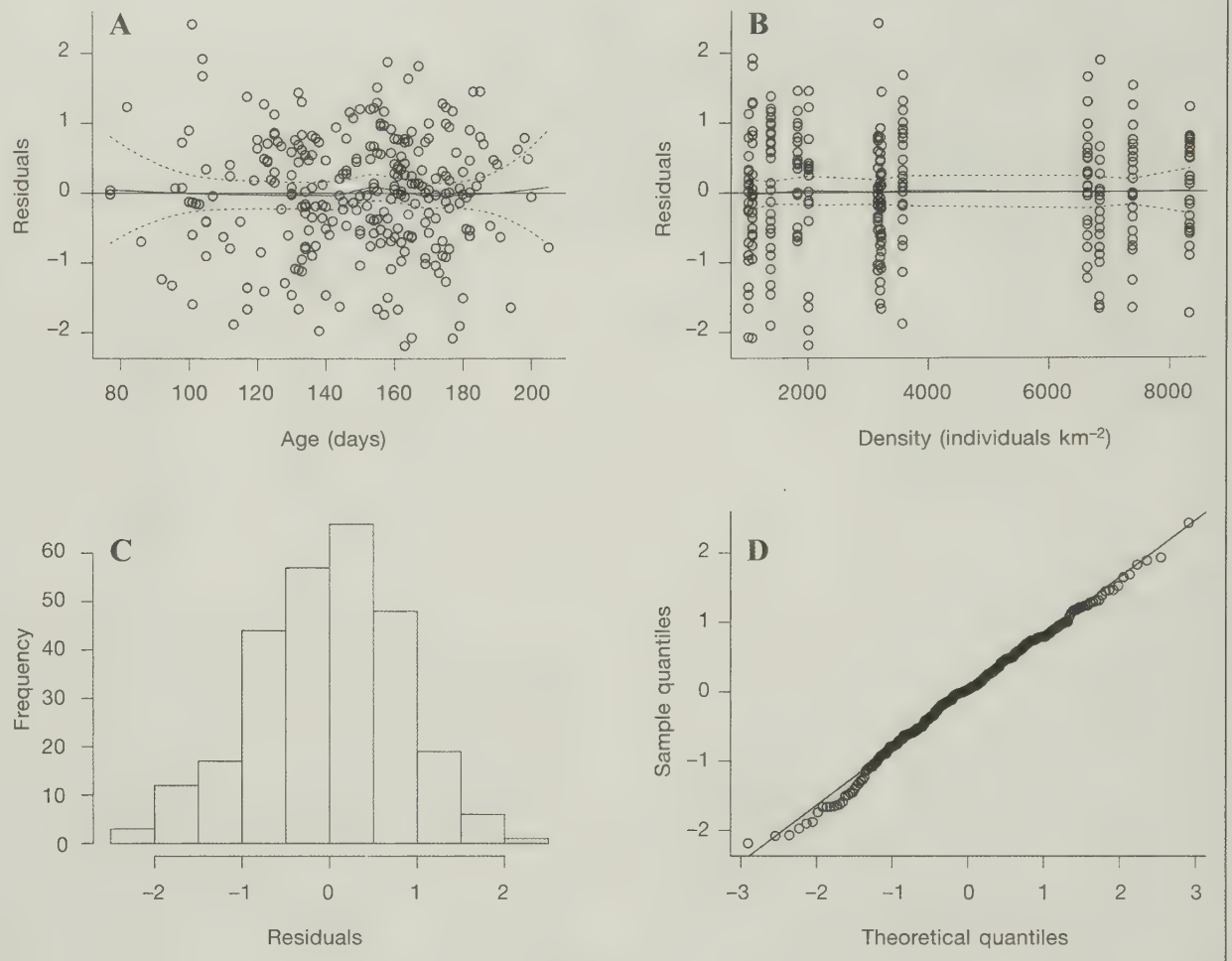

Figure 7

Graphs for the validation of the best model of the generalized additive model in age and fish density were used as explanatory variables. Residuals versus explanatory variables were (**A**) age and (**B**) density to assess homogeneity and (**C**) a histogram of residuals and (**D**) a Quantile-Quantile (Q-Q) plot to assess normality. The model was developed from data for recruits of European hake (*Merluccius merluccius*) caught in June 2011 during the Mediterranean International [bottom] Trawl Survey (MEDITS) in the Ligurian Sea and northern Tyrrhenian Sea.

presents a potentially valuable feature for conservation and management purposes—one that, for instance, could be leveraged to ensure long-term effectiveness of no-take areas: Colloca et al. (2009) estimated that the closure of highly persistent nurseries would result in a small reduction of the exploitable fishery area (around 5%) and the protection of a considerable fraction (40%) of the estimated total number of recruits.

In a recent study, Cannella et al. (2011) found high hepatosomatic index values, a proxy for body condition, in recruits of European hake from areas of high density in the Tyrrhenian Sea, support the hypothesis that high-density nurseries around the shelf break are high-quality areas where juveniles find environmental conditions of food and temperature that are appropriate for survival and growth.

The present study is limited to growth estimation from a single year. However, although a longer time series of multiyear data is needed to sufficiently understand the role of environmental variables and density-based factors on growth, the results from the present study provide a first baseline and rationale in corroborating the key role played by high-quality nurseries for recruitment success. The results from this study indicate that European hake recruits grow faster inside their main nurseries than outside them, thereby increasing their chance to survive before they migrate to shallower areas on the continental platform. According to the definition by Dahlgren et al. (2006), these areas can be regarded as "effective juvenile habitats." In the areas that were identified as effective juvenile habitats, environmental characteristics (e.g., food avail-

ability and protection to predation) enhance juvenile condition and growth.

Juveniles of European hake are exposed to trawl fisheries after bottom settlement in their nursery grounds. Therefore, a reduction in fishing mortality of immature fish could be a fundamental prerequisite for sustainable fisheries. The implementation of the following requirements—use of a large mesh size, square-mesh panels, and selection grids in trawl fisheries—has reduced the bycatch of juvenile European hake (Sardà et al., 2004; Lucchetti, 2008). However, these measures may not be sufficiently effective in protecting juveniles and nursery areas. In fact, the use of gear selectivity as a fishery management tool without adequate research into the fate of escaping juvenile fish should be cause for concern for any fishery (Chopin and Arimoto, 1995). Moreover, trawling activities are known to cause alterations to the bottom of the seafloor, reducing habitat complexity and altering benthic community structure (Kaiser et al., 2002), both of which are fundamental components of habitat for juvenile European hake. Therefore, a deeper understanding of the importance of the quality of recruitment habitats (i.e., nurseries) on the growth and the survival of juveniles of European hake is a challenging task that could be relevant for conservation purposes (e.g., protection of nursery grounds).

Acknowledgments

The authors are grateful to the 3 anonymous reviewers for their comments and suggestions, which contributed to improvement at the manuscript stage.

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Ecological effects of bottom trawling on the structural attributes of fish habitat in unconsolidated sediments along the central California outer continental shelf

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Abstract—Bottom trawling has been shown to affect the seafloor and associated biological communities around the world. Considerably less is known about the dynamics of impacts to structural attributes of fish habitat, particularly in unconsolidated sandy sediments of the continental shelf. We collaborated with commercial fishermen to conduct experimental trawls, with the type of small-footrope trawl required for trawling on the continental shelf, along the 170-m isobath in an area off Morro Bay in central California. The bottom trawling intensity we applied was based on the historical range of fishing effort in the study area and included low-intensity and high-intensity treatments. A remotely operated vehicle was used to collect continuous video and still photographs in trawled and in untrawled control plots, before trawling and at 2 weeks, 6 months, and 1 year after trawling. Scour marks from the heavy doors of the trawl were observed in the seafloor and persisted for at least a year. Although data extracted from the collected imagery showed some smoothing of the seafloor in trawled plots, the minimal differences between trawled and control plots in microtopographic structure on the seafloor were statistically significant only during one sampling period. Further, there were no significant differences between trawled and untrawled plots with respect to structure-forming invertebrates (e.g., sea whips) and mobile invertebrates (e.g., sea stars). The results of our study, part of ongoing efforts to understand and manage fishing impacts, indicate that bottom trawling with a small-footrope gear may have limited effects in some sand habitats.

Manuscript submitted 28 August 2013.
Manuscript accepted 12 December 2014.
Fish. Bull. 113:82–96 (2015).
doi: 10.7755/FB.113.1.8

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

The ecological effects of bottom trawling on continental shelves have been documented in several regions of the world (see reviews in Dayton et al., 1995; Kaiser et al., 1998; Watling and Norse, 1998; Auster and Langton, 1999; NRC, 2002). These effects include overfishing (NRC, 1999; Jackson et al., 2001) and bycatch (Alverson et al., 1994; De Alteris et al., 2000; Machias et al., 2001; Anderson and Clark, 2003), as well as impacts to structural attributes of the seafloor (Auster et al., 1996; Lindholm et al., 2004). Indeed, bottom trawling has been described as the most significant impact on marine ecosystems below the effective depth of storm penetration (Dayton et al., 1995; Watling and Norse, 1998; NRC, 2002).

In the context of impacts to the seafloor, it has been established that bottom trawling can smooth bedforms (Hall, 1994; Schwinghamer et al., 1998), remove structure-forming invertebrate fauna (the bodies of such organisms provide habitat structure) (Auster et al., 1996; Collie et al., 1997; Kaiser et al., 2000; Koslow et al., 2001), and remove structure-building organisms that create habitat (such as depressions in the sediment), as a result of their normal behavior (Auster and Langton, 1999). Bedforms and habitat features formed or created by organisms are used by fishes at a variety of life history stages as refugia from predators and bottom currents (Auster et al., 1991; Auster and Langton, 1999; Stoner and Titgen, 2003).

Observations of the use of sandwave habitats on Georges Bank and

in the western Gulf of Maine by silver hake (*Merluccius bilinearis)* indicate a strong correlation between individual fish size and sand-wave period; smaller fishes use smaller sand waves (Auster et al., 2003a). Acadian redfish (*Sebastes fasciatus*) have been seen to have ontogenetic shifts from physical attributes (piled boulder reefs) of the seafloor at early life history stages to structure-forming invertebrates (erect Cerianthid anemones) found in adjacent soft sediment habitats at late-juvenile stages (Auster et al., 2003b). Sea pens (of the order Pennatulacea) have been shown to harbor fish larvae, potentially playing an important role in the early life history of some redfishes (*Sebastes* spp.) (Baillon et al., 2012). Sea whips have also been observed to harbor dense aggregations of Pacific ocean perch (*Sebastes alutus*) in the Bering Sea (Brodeur, 2001). In California, Hallenbeck et al. (2012), using a remotely operated vehicle (ROV), found higher densities of small fishes and invertebrate fauna inside naturally occurring rippled scour depressions than densities in low-relief habitats outside these depressions. These features are now known to occur across the continental shelf of California in sandy substrates (Davis et al., 2013). Further, structural attributes of the seafloor have been shown to enhance survival of postsettlement demersal fishes, both in laboratory experiments (Lindholm et al., 1999) and in field studies (Tupper and Boutilier, 1995).

Literature on the ecological effects of bottom trawling has grown over the past twenty years. There is some evidence that low-relief sandy environments recover more quickly after cessation of trawling than higher-relief hard substrates and the fauna associated them (NRC, 2002; Barnes and Thomas, 2005). The dynamics of recovery from trawling within soft sediments are less clear. Studies in which bottom grabs were used to sample organisms in unconsolidated sediments have revealed a measurable impact from trawling on an infaunal community in the North Sea from a single pass of a beam trawl, even in an environment that had been trawled heavily for decades (Reiss et al., 2009), but in a study in South Africa, no measurable impacts of additional trawling to the epifaunal community in a continuously trawled area (Atkinson et al., 2011). On Georges Bank, Lindholm et al. (2004) observed trawling impacts to sand habitats below the 60-m isobath in imagery collected with a video drift camera, but no impact was evident at depths shallower than 60 m in sand habitats, where grain sizes were similar to those in the deeper habitats where regular storm and tidal currents re-sorted the sediment. Important questions remain, particularly with respect to the effects of bottom trawling on the structural attributes of seafloor habitat in unconsolidated sediments.

Insight into the ecological effects of bottom trawling in unconsolidated sandy sediments is particularly important for California, where more than 80% of the continental shelf comprises sand (Allen et al., 2006) and bottom trawling has been an important component of the groundfish fishery. However, a limitation common to the few existing studies of impacts of trawling along the West Coast of the United States (Engel and Kvitek, 1998; Freese et al., 1999; McConnaughey et al., 2000; Hixon and Tissot, 2007; de Marignac et al., 2009) was the fact that trawling effort was not controlled as part of these studies. These studies, although instructive, have been either 1) snapshots based on data collected after trawling, 2) studies with little knowledge of the intensity of trawling effort in the area studied, or 3) both. Available historical data on the distribution of trawling rarely exist, especially with the level of precision in georeferenced track lines that are critical for the accurate quantification of impacts to the seafloor; most available historical data occur as averaged estimates of trawling intensity across large areas (Bellman et al., 2005; Mason et al., 2012).

California has a long history of bottom trawling, and many ports have relied on landings of trawl-caught groundfishes. However, because of various regulatory and socioeconomic factors, trawling effort has shifted spatially and has diminished in recent years (Bellman et. al., 2005; Mason et. al., 2012). Regulations on the design of bottom-trawl gear have resulted in much of the effort shifting away from rocky habitats (Bellman et al., 2005). One regulation in particular restricted the diameter of trawl footrope gear that was allowed for use along the continental shelf. This regulation, enacted by the Pacific Fishery Management Council in 2000, required trawl vessels to use small-footrope gear (≤20 cm in diameter) along the continental shelf, therefore, inhibiting the use of large-footrope gear that can pass over rocky terrain (Dalton, 1999). The level of trawling effort (number of active trawl permits) has also been reduced over the last decade because of a federal trawl buy back, and private purchase of trawl permits in the Central Coast (Gleason et al., 2009). The trawl fishery recently transitioned to an individual transferable quota (ITQ) system, and there is increasing use of nontrawl fixed gear that produces consistently higher prices for groundfishes and is intended to reduce bycatch of overfished species. However, trawling is still the primary way to catch flatfish and remains an important component of California fisheries (Hilborn et al., 2012).

The type and intensity of impact of bottom trawling on the seafloor and associated ecological communities are significant for effective management of trawling activities. As of this writing, state and federal management agencies have implemented closures of broad areas; these closures have limited the current trawling but also have constrained commercial fisheries and reduced landings and local seafood supply (Hilborn et al., 2012). A ban on trawling in California state waters, with the exception of some halibut trawl grounds, was implemented through state legislation that was enacted in 2004 (Calif. State Legislature, 2004). The Rockfish Conservation Area (RCA), established from 2002 to 2007 and extending from northern Washington to southern California, excludes trawling to help re-

building efforts for overfished stocks and has resulted in displacement of some trawling effort (Bellman et al., 2005). Federal closures for trawl fishing in additional areas were established in 2006 to protect essential fish habitat (Copps et al., 2008; Gleason et al., 2013). Together, these closures to trawling protect 61% of shelf and slope habitat from bottom trawling in central California, between Point Conception and Point Reyes from the shore to a depth of 2000 m).

In this study, we collaborated with members of the commercial fishing industry to conduct experimental trawling with small-footrope gear at known intensities in the unconsolidated sediments of the outer continental shelf off Point Buchon and Morro Bay in central California. This directed trawling allowed us to quantify, with a high degree of confidence, the impacts to physical and biological attributes of fish habitat in the study area.

Materials and methods

Data collection

The primary study area was located on the outer continental shelf off Point Buchon and Morro Bay (Fig. 1). This study area was selected after discussions with members of the commercial fishing industry in Morro Bay and was situated immediately shoreward of the federal RCA at the shelf-slope break in a location that was historically trawled for flatfish, such as the petrale sole (*Eopsetta jordani*) and Dover sole (*Microstomus pacificus*). The study area had not been trawled commercially since before 2000, according to vessel monitoring system data (Mason[1]; Mason et al., 2012). Prospecting with an ROV in 2008 and multibeam sonar in 2009 revealed that the area comprises low-relief, unconsolidated sediments. Our study was conducted between 2009 and 2012; in 2012, additional surveys were conducted with an ROV along transects to the north and south of the study area to compare different substrates and biological communities at other locations along the shelf (Fig. 1).

Along the 170-m isobath, 8 paired study plots were identified (Fig. 1). Each plot measured approximately 1000 m by 300 m, and 500 m separated each adjacent plot. Plots were numbered from 1 to 8 consecutively from north to south; plots 3, 4, 7, and 8 were experimentally trawled plots, and plots 1, 2, 5 and 6 were untrawled (or control) plots.

Experimental trawling

All trawling activities were conducted aboard FV *South Bay*, a 16.8-m trawler that operated from Morro Bay. The *South Bay* was equipped with a bottom trawl that had a small footrope, in accordance with gear requirements under federal regulations for trawling shoreward of the RCA. The trawl design consisted of a 2-bridle trawl with a fishing circle of 300 meshes and a mesh size of 11.6 cm. The funnel tapered down to the codend at a 2:1 cutting ratio, and the mesh size at the codend was 11.4 cm. The footrope was configured with "mudgear" discs that measured 20.3 and 10.2 cm in diameter. The larger 20.3-cm-diameter discs were spaced evenly along the footrope at 1-m intervals, allowing the smaller 10.2-cm-diameter discs to ride above the seafloor. The net was held open by trawl doors, each measuring 1.1 by 1.4 m and weighing approximately 315 kg. Trawling operations were conducted at a speed of 2.1 knots, which is the speed typically used to harvest most flatfishes and soles (Bothidae and Pleuronectidae) in the federal groundfish fishery. An exception to this typical speed is that speeds of 3.0–4.0 knots are used to harvest California halibut (*Paralichthys californicus*) in the state-managed fishery for that particular species. At the speed used for this study, the trawl doors spread the net width to 55 m and the net height to 2.4 m.

Experimental trawling operations were divided into 2 treatments according to intensity of effort: low intensity and high intensity. The 2 treatments were designed to broadly reflect the range of effort applied historically to the seafloor in the study area, on the basis of published records (Mason et al., 2012) and unpublished data collected by NOAA Fisheries (Mason[1]). The number of trawl passes per treatment was calculated by using the width of the study plots and the width of the trawl doors on the seafloor when underway. The low-intensity treatment (October 2009) featured enough passes through the study plots to ensure that every square meter of each plot was trawled 3 times. The high-intensity treatment (October 2010) doubled that effort on the same plots so that each plot was impacted an additional 5 times, for a total of 8 passes. For logistical reasons, the high-intensity trawling effort was applied to the previously trawled plots and, therefore, reflects 2 years of directed trawling. To minimize the number of times the trawl gear was deployed and recovered during each treatment and to avoid accidentally trawling in control plots, adjacent plots were paired such that the trawl would remain on the seafloor from the beginning of plot 3 to the end of plot 4, and the same protocol followed at plots 7 and 8 (Fig. 1).

Imagery collection

Video and still imagery of the seafloor were collected with a Vector L4 ROV (Deep Ocean Engineering, Inc., San Jose, CA) equipped with 3 georeferenced cameras (forward-looking video, down-looking video, and digital still camera), 2 quartz halogen and 2 hydrargyrum medium-arc iodide lights, paired forward- and down-looking lasers, and a strobe for enhancement of still photographs. The ROV was also equipped with an altimeter and forward-facing multibeam sonar. The position of the ROV on the seafloor was maintained with

[1] Mason, J. 2008. Personal commun. Pacific Fisheries Environmental Laboratory, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, Pacific Grove, CA 93950.

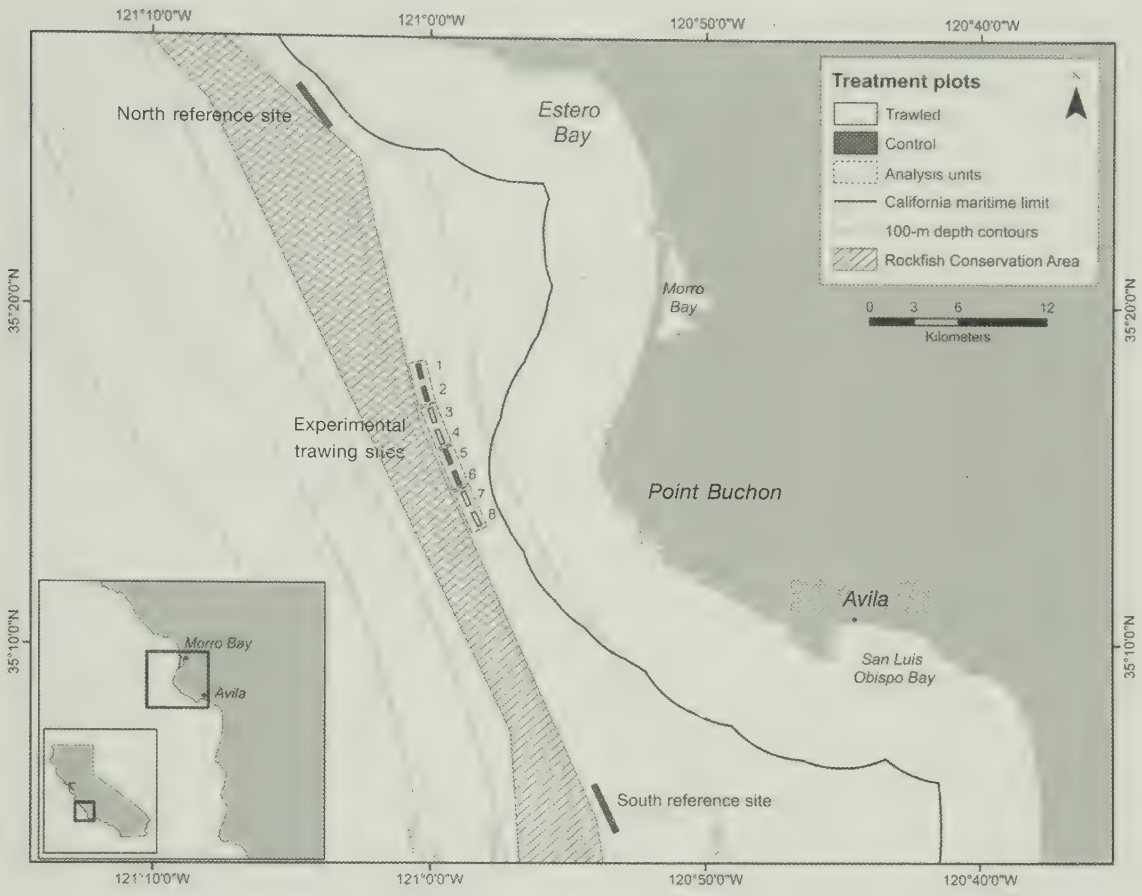

Figure 1

Map of the study area in waters off Point Buchon and Morro Bay in central California, where 4 control plots (black) and 4 trawled plots (white) were sampled between 2009 and 2012 and grouped into 4 analysis units (dotted lines). North and south reference sites (shown) were sampled in May 2012. Also included are the state waters boundary (black line) and the extent of the Rockfish Conservation Area (hatched area).

a Trackpoint 3 acoustic positioning system (EdgeTech, West Wareham, MA) and the resulting coordinates were logged into Hypack navigational software, vers. 2010 (Hypack, Inc., Middletown, CT). The ROV was "flown" over the seafloor at a mean altitude of 0.8 m and a speed of approximately 0.6 knots.

A before-after-control-impact (BACI) sampling design was employed for these visual surveys. Surveys of the 8 study plots were conducted with the ROV in September 2009, immediately before the low-intensity trawling treatment. Subsequent ROV surveys were conducted 2-weeks after trawling (November 2009), 6 months after trawling (April 2010), and 1 year after trawling (September 2010). Visual surveys were again conducted with the ROV at 2-weeks (November 2010), 6 months (May 2011), 1 year (September 2011), and 1.5 years (May 2012) after the high-intensity trawling. During the final ROV surveys in May 2012, 3 additional transects were surveyed at similar depths to the north and south of the study area (Fig. 1) to explore the extent to which the substrate and biological community in the study area was reflective of the broader region of the central California coast.

During each sampling period, 3 transects in each study plot were surveyed with an ROV. Each ROV transect measured approximately 300 m in length (20 min in duration) as determined by species and habitat accumulation curves plotted from data collected previously in soft sediment communities (Lindholm et al., 2004, 2009; de Marignac et al., 2009) and from a review of preliminary data collected in the study area in the fall of 2008. Surveys were initiated on transects randomly from a set of pre-existing starting points located at either the northwest or southeast ends of each study plot. Determination of the starting point of a plot depended on local conditions at the time of the dive so that any effect of currents and wind was minimized. After the starting point of a plot was determined, a random number generator selected a starting point from among twenty potential points, and the ROV subsequently followed the 170-m isobath across the long axis of the study plot.

Digital still photographs were taken at 1-min intervals along each transect for a minimum of 20 photographs. Each still photograph covered an area of approximately 0.42 m^2. Paired, parallel, down-looking lasers (spaced 10 cm apart on the ROV) provided a consistent reference for still photographs to maintain constancy in area of coverage for each image and to size individual organisms where possible. Still photographs were used to assess the primary metrics of the study, namely 1) the percent cover of microtopographic features, meaning the proportion of the seafloor that had an elevation, burrow, or other microtopographic feature, 2) density of structure-forming macro-invertebrates, and 3) density of selected mobile macro-invertebrates.

From our observations across multiple ROV surveys, we determined that the microtopographic complexity in the unconsolidated sandy sediments at the study depths primarily resulted from bioturbation. Bioturbation in this context refers to deviations from the plane of the sediment–water interface (such as ridges and mounds, burrows and hole) created by the movement of organisms such as sea stars and fishes or organisms such as mud urchins through the upper centimeters of the sediment. Small features that result from bioturbation can serve as habitat for demersal fishes from a variety of species, including many flatfishes found in the study area. Digital still photographs were used to quantify the spatial extent of microtopographic features (i.e., bioturbation) in each of the 8 study plots. The percent area covered was quantified for each still photograph with a digitally rendered grid that was 5 by 5 cm and was superimposed over each photograph. Any cell in which a microtopographic feature was evident was counted.

Digital still photographs also were used to quantify the density of benthic invertebrate species in each study plot. Structure-forming organisms (such as those found in the study area, primarily sea pens, sea whips, and anemones) are erect, mostly sedentary creatures that extend above the plane of the sediment and provide potential habitat structure for fishes and mobile invertebrates. Mobile organisms, including crabs, urchins, and sea stars, move along and across the plane of the sediment, providing transient habitat themselves (e.g., for small fish seeking cover adjacent to larger sea stars) and altering the sediment itself, as described previously. Densities of both structure-forming and mobile invertebrates were extracted from digital still photographs. Every organism that occurred in still photographs was counted and identified to the lowest taxonomic level possible and then grouped by taxon or mobility for analyses.

Data analyses

Although a BACI sampling design was planned (similar to the one used by Pitcher et al., 2009) with 8 randomly distributed plots, the limitations, described previously, in the distribution of trawling effort across those plots required that we alter our analytical approach. To optimize our ability to detect statistical differences among paired plots and across years and to reduce the probability of a type-II error, we randomly selected 50 photographs from each of 4 pairs of adjacent plots for each treatment (identified as analysis units in Fig. 1) so that independent samples would be distributed across the entire study area and across time. This practice effectively reduced the number of replicates for each treatment from 4 plots to 2 pairs of adjacent plots and allowed for a greatly improved number of samples (N), when compared with a transect-based approach: N=1600 for treatment-wide analyses, and N=200 for year-to-year comparisons. This approach also reduced the effect of spatial autocorrelation in data collected along sequential transects and eliminated any inflated statistical significance due to psuedoreplication (Hurlbert, 1984).

We used the 2-proportion Z-test to determine whether the hypothesized difference between population proportions (arcsine transformed) in microtopographic structure varied significantly between trawled and control plots and within treatments (high-intensity or low-intensity trawling effort) over time. T-tests were used to test for any differences in the densities of structure-forming macroinvertebrates and mobile macroinvertebrates between trawled and control plots and within treatments over time. Post-hoc power analyses were conducted with the statistical program R, vers. 3.1.0 (R Core Team, 2014) on the Z-test and t-tests for the 3 primary metrics to evaluate the power of each test to detect significant differences, particularly given the low densities observed for sessile, structure-forming invertebrates and for mobile invertebrates.

Results

From September 2009 to May 2012, ROV surveys were completed along 297 transects in the study area, and 6200 still photographs were taken on transects (an additional 11,000 photographs were taken to support species identifications and to capture unique features). From those still photographs, we extracted data on 38 invertebrate species from 5 phyla—anthozoans (10), echinoderms (11), molluscs (11), crustaceans (3), and annelids (3). Polychaete worms (*Chloeia pinnata*) were numerically dominant, followed closely by several species of brittle stars (phylum Echinodermata: class Ophiuroidea), all of which occurred on the surface of the sediment in dense but spatially and temporally variable patches.

Temporal and spatial variability

Although overall density of these observed species was low (fractions of individuals per square meter) in the study area, temporal variability in the densities of selected invertebrate taxa was considerable across sam-

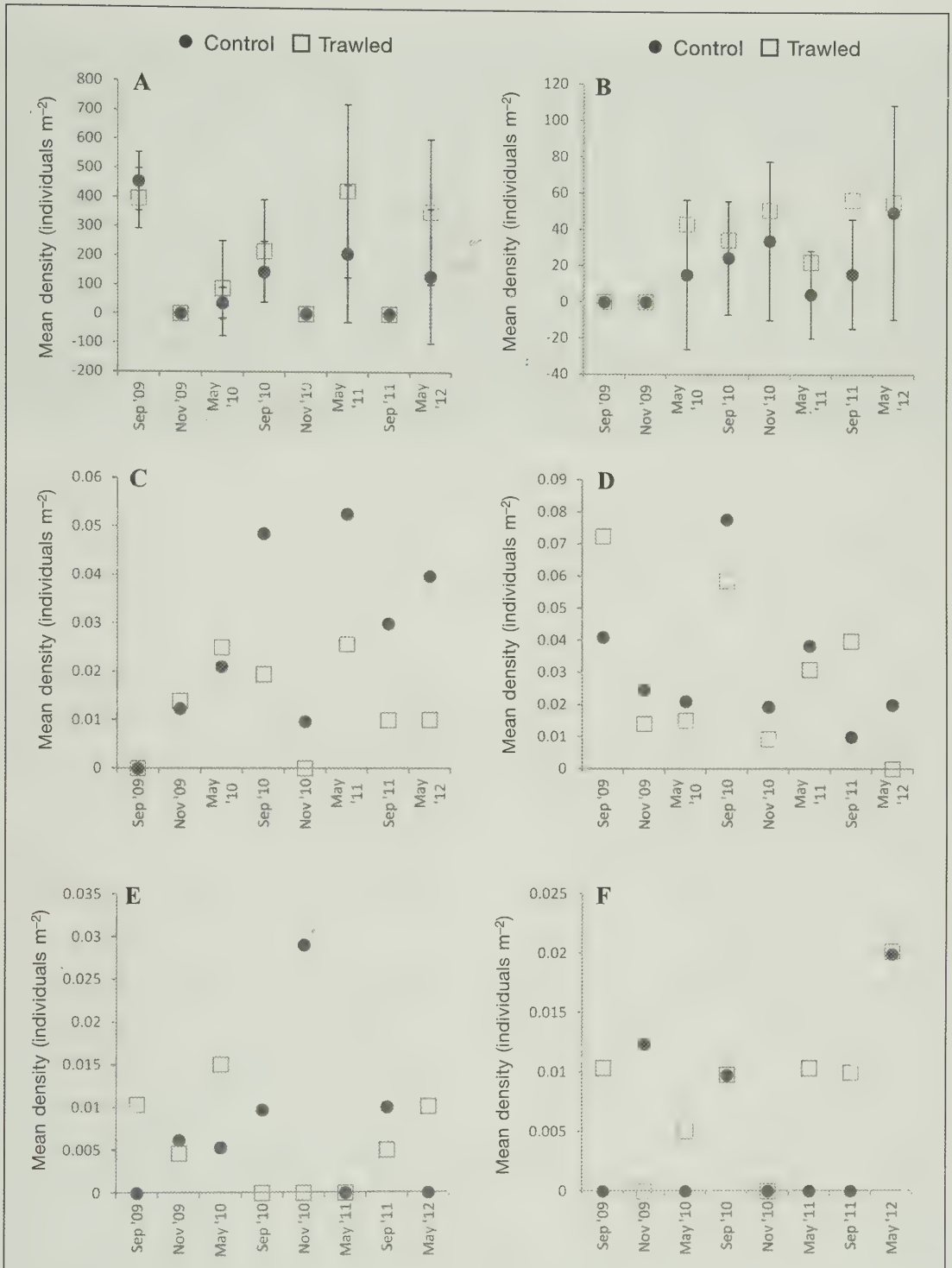

Figure 2

Temporal variability in mean density (individuals m^{-2}) of 6 members of the invertebrate community found in the study plots, both control (untrawled) and trawled surveyed off central California between 2009 and 2012. The 6 groups of invertebrates shown are (**A**) scale worms (polychaetes), (**B**) brittle stars (ophiuroids), (**C**) sea slugs (notaspidean), (**D**) octopuses (octopods), (**E**) squids (teuthids), and (**F**) sea stars (asteroids). Note that the scale on the *y*-axis differs among plots. Indicated with error bars, 95% confidence intervals are provided for the organisms with densities >10 individuals m^{-2} (worms and brittle stars).

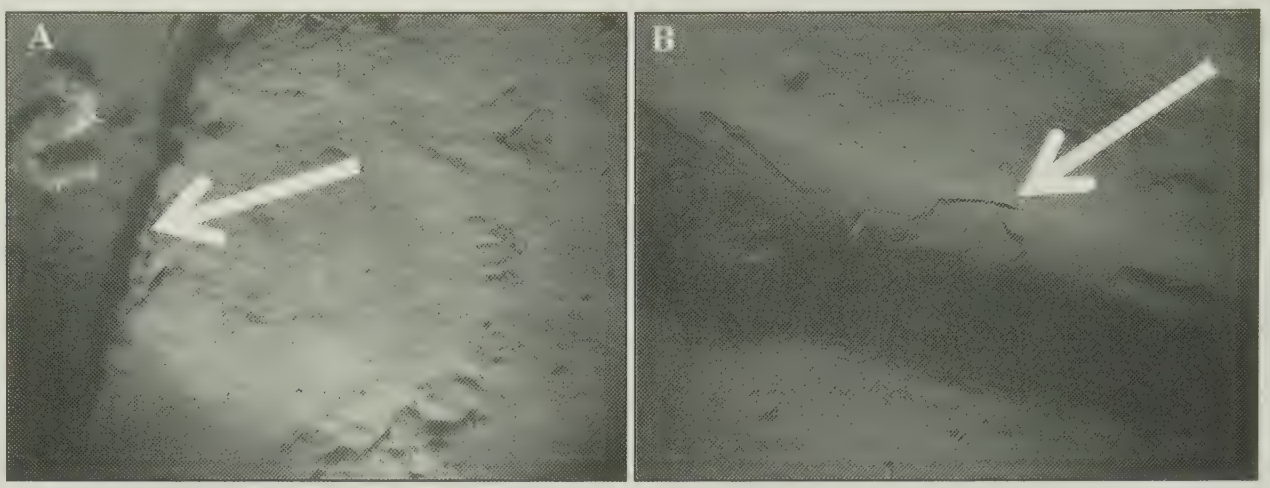

Figure 3

Photographs of scour marks created by doors of the bottom trawl used in this study conducted off central California. Images were taken (**A**) in November 2009, immediately after low-intensity trawling, and (**B**) in September 2010, 1 year after low-intensity trawling.

pling periods and seasons (Figs. 2, A–F). The densities of polychaete worms (Fig. 2A) peaked during 3 separate sampling periods during 2 separate seasons; the largest peak (480 individuals m^{-2}) occurred in September 2009, followed by smaller peaks in May 2011 (430 individuals m–2) and May 2012 (390 individuals m–2). No polychaetes were observed in either November 2009 or November 2010. Occurrence of brittle stars (Fig. 2B) was observed at much lower densities. For example, absent from the study area in September and November 2009, brittle stars were present during every other sampling period, peaking at 60 individuals m–2 in September 2011. Other organisms, including notaspideans (Fig. 2C), octopods (Fig. 2D), teuthids (Fig. 2E), and asteroids (Fig. 2F) were present in very small, although variable, densities over the course of our study.

In the broader study area, the north reference site (Fig. 1) had an assemblage of sessile invertebrates that was similar to the assemblage in the primary study area, including sea whips (*Halipteris* spp.), sea pens (*Ptilosarcus gurneyi*, *Pennatula* spp., and *Stylatula* spp.), and anemones (Halcampidae, *Urticina* spp., and *Pachycerianthus fimbriatus*). The south reference site had invertebrates that were more mobile, primarily ocean shrimp (*Pandalus jordani*), that were rarely observed in the study plots. However, it should be noted that the amount of recent trawling effort in the north and south reference sites was unknown.

Low-intensity trawling

Trawl doors can create scour marks (or troughs) in the sediment as they are towed along the bottom of the seafloor. Scour marks from the low-intensity trawling effort were clearly evident in the sediment immediately after the directed trawling (Fig. 3A) and were still present 1 year after trawling in September 2010 (Fig. 3B). Demersal fishes, mobile invertebrates, and drift kelp were all observed in and immediately adjacent to these scour marks.

The mean percent cover of microtopographic features was similar between the trawled and control plots in September 2009 before the directed trawling, at 75% and 72%, respectively (Fig. 4A). Immediately following the low-intensity trawling treatment, the percent cover of microtopographic features in control and trawled plots diverged but did not differ statistically (Z=0.109, P=0.460). The mean percent cover of microtopographic features in the trawled plots declined by 15%. Interestingly, the percent cover also declined after trawling in the control plots, although by an amount (9%) lower than the decrease in the trawled plots. The small but insignificant difference in complexity (Z=0.096, P=0.464) between trawled and control plots persisted at 6 months after trawling, but values in both types of plots stabilized. In August 2010, at 1 year after trawling, the mean percent cover of microtopographic features declined in both groups of plots over the 6-month period (15% and 17% in control and trawled plots, respectively) but were not significantly different (Z=0.156, P=0.440). The cumulative decline in mean percent cover at 1 year after trawling was –24% and –31% in control and trawled plots, respectively.

The densities of both sessile, structure-forming (Fig. 4B) and mobile (Fig. 4C) macro-invertebrates were very low in both trawled and control plots before and after

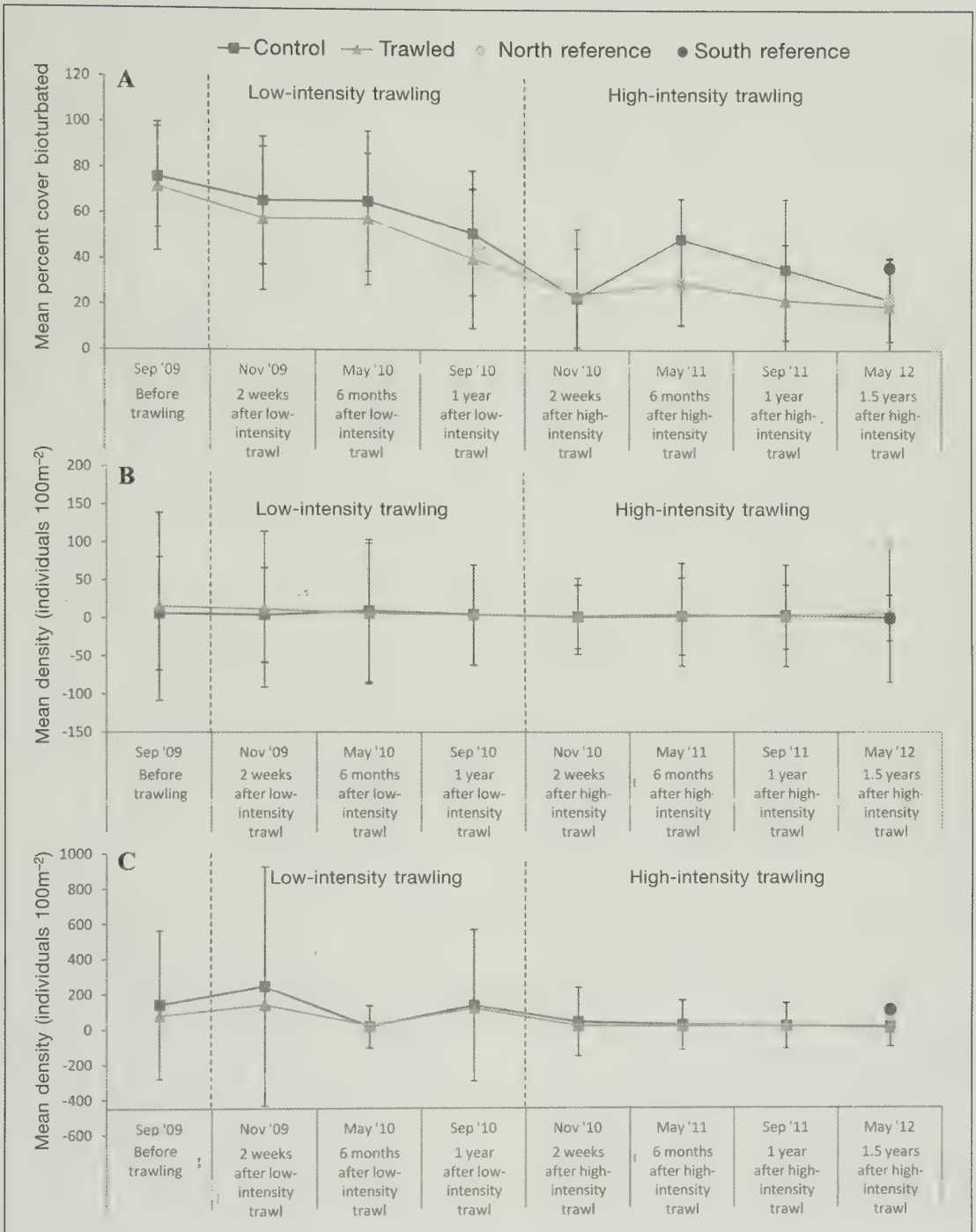

Figure 4

Results from visual surveys conducted with a remotely operated vehicle between 2009 and 2012 at control (untrawled) and trawled plots before and after low- and high-intensity experimental trawling across the primary study area in waters off Point Buchon and Morro Bay in central California: (**A**) percent cover of microtopography with bioturbation, (**B**) density of sessile invertebrates, and (**C**) density of mobile invertebrates, Also shown are values from surveys completed in May 2012 at reference sites north and south of the main study area. Error bars indicate 95% confidence intervals.

low-intensity trawling. The densities of sessile invertebrates, which peaked at 2.3 individuals 100 m–2, were not significantly different between trawled and control plots at any point over the study period. The densities of mobile macro-invertebrates were higher, peaking at 220 individuals 100 m^{-2} but did not differ significantly between trawled and control plots after low-intensity trawling activities.

High-intensity trawling

Scour marks were immediately visible on the substrate during visual surveys conducted 2 weeks after high-intensity trawling—an observation consistent with those of the condition of the seafloor after low-intensity trawling. The mean percent cover of microtopographic complexity features (Fig. 4A) was not significantly different between the trawled and untrawled plots in August 2010, 1 year after low-intensity trawling and approximately one month before the directed trawling in the same study plots at a higher intensity. Immediately after high-intensity trawling, the mean percent cover microtopographic features in both control and trawled plots declined precipitously, 27% and 25% respectively, but did not differ statistically (Z=0.015, P=0.496).

However, in May 2011, at 6 months after high-intensity trawling, the mean percent cover of microtopographic features had increased in both trawled and control plots, and a significant increase of 24% in the control plots versus 4% in the trawled plots (Z=2.802, P=0.003). At 1 year after trawling, the mean percent cover had declined again in both types of plots to 37% in control plots and 27% in trawled plots and did not differ statistically (Z=0.675, P=0.251). In May 2012, approximately 1.5 years after trawling, mean percent cover had declined further in both control and trawled plots to 22.2% and 19.4%, respectively. The overall decline in mean percent cover of microtopographic features after the cumulative impact of both low- and high-intensity trawling was –53.96% and –52.43% in control and trawled plots, respectively.

The densities of both structure-forming (Fig. 4B) and mobile (Fig. 4C) macroinvertebrate organisms continued to be very low in both trawled and control plots after high-intensity trawling. The densities of structure-forming invertebrates, which peaked at 0.026 individuals 100 m^{-2} in the control plots, were not significantly different between trawled and control plots at any point of the study period. The densities of mobile macroinvertebrates did not differ significantly between trawled and control plots after high-intensity trawling activities.

Power analyses

The results of power analyses (Fig. 5) for our revised sampling design for both overall comparisons (N=1600) and year-to-year comparisons (N=200) indicated that our ability to detect an impact from trawling on microtopographic structure with the Z-test was substantial and, therefore, that even a small effect (0.2, as per Lipsey, 1990) would be clearly discernible. That high power declined very little with the t-tests (Fig. 5) for identification of trawling effects on the densities of both structure-forming and mobile macro-invertebrates.

Discussion

We aimed to quantify impacts of bottom trawling on the structural attributes of fish habitat in unconsolidated sandy sediments on the continental shelf off central California. The persistence of scour marks from the doors of the small-footrope bottom trawl was the primary impact observed in our study. Some smoothing of microtopographic structure on the seafloor was observed in the trawled plots compared with control plots (as measured by reductions in the percentage of the seafloor that was observed to have bioturbation). However, the minimal differences in microtopographic structure were statistically significant only during one of 8 sampling periods over the course of this study. Further, even with a high statistical power to discern such effects, no impacts from bottom trawling were observed in the densities of sessile, structure-forming invertebrates, declines of which are a common indicator of trawling impacts on fish habitat in other studies worldwide (Auster and Langton, 1999; Kaiser et al., 2002; Barnes and Thomas, 2005; Hiddink et al., 2007). Given the considerable variability observed in the densities of mobile macro invertebrates in the study area, no significant differences attributable to trawling existed between trawled and control plots.

Microtopographic features on the seafloor have been shown to provide habitat for demersal fishes of a variety of species (Auster et al., 1995; Auster et al., 1997; Malatesta and Auster, 1999; Tissot et al., 2006), creating the potential for larger, population-scale impacts from bottom trawling (Lindholm et al., 2001; Rooper et al., 2011). Much of the global literature on the effects of bottom trawling has focused on hard substrates (NRC, 2002) and associated high-relief structural attributes (Freese et al., 1999; Henry et al., 2006; Stone, 2006; Hiddink et al., 2006; Althaus et al., 2009). The comparatively limited structural attributes in low-relief, unconsolidated sediments (such as sand waves and depressions or burrows) still can provide important refugia for fishes (Auster et al., 1997; Gerstner, 1998; Gerstner and Webb, 1998; Sanchez et al, 2000).

We expected that impacts to the structural attributes of fish habitat, including physical (microtopographic) and biological (densities of structure-forming invertebrate) features would be discernible by a difference between control and trawled plots after low-intensity bottom trawling and that the difference would increase following high-intensity trawling. These predictions were based on our understanding of seafloor impacts from other studies (Auster et al., 1996; Engel and Kvitek, 1998; Hixon and Tissot, 2007; de Marignac et al.,

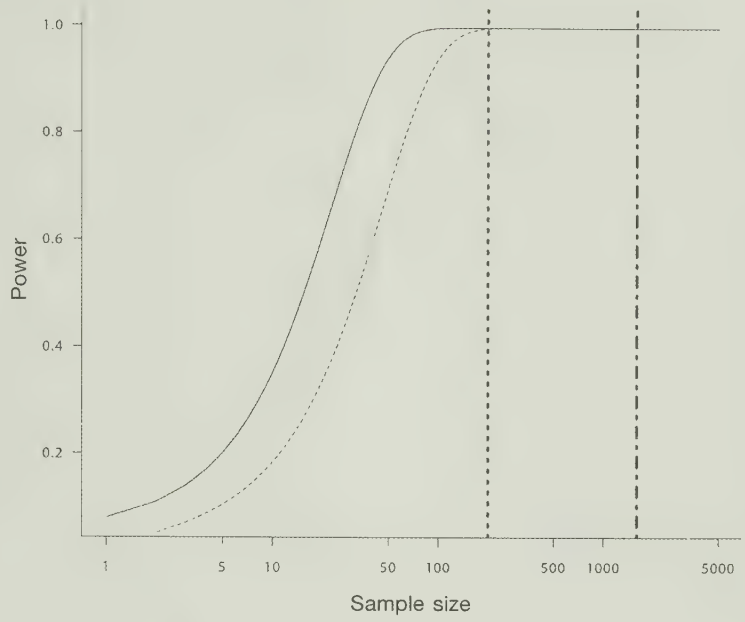

Figure 5

Power curves for *Z*-test conducted on percent cover of microtopographic features (solid curve) and *t*-tests conducted on densities of sessile and mobile invertebrates (dotted curve) from surveys conducted off central California between 2009 and 2012. The *x*-axis was log transformed to resolve differences between the 2 curves. The sample size for all 3 metrics is also provided for overall tests (vertical dashed and dotted lines) and interannual comparisons (vertical dotted line).

2009), global reviews (e.g., Auster and Langton, 1999; Hall, 1994; NRC, 2002; Barnes and Thomas, 2005), and the fact that, at a depth of 170 m, the entire study area was well below the effective depth of storm penetration. For instance, elsewhere along the central coast of California, approximately 375 km to the north of Morro Bay, de Marignac et al. (2009) conducted a study at similar depths and with similar substrate composition and found that numbers of biogenic mounds and depressions were significantly higher in a recovering area than in an area that continued to be actively trawled.

Yet the expectation of clearly discernible impacts on the seafloor was largely not borne out by the results of our study. After low-intensity trawling, the small but persistent difference in the microtopographic complexity of the seafloor between control and trawled plots was indicative of an impact from bottom trawling. We attributed this difference to the smoothing of habitat features by the trawl footrope as it passed over the bottom of the seafloor (Auster and Langton, 1999), as well as to the removal of the mobile organisms responsible for bioturbation of the sediment (Lohrer et al., 2004; Meysman et al., 2006). However, the difference was not statistically significant in our analyses, despite a high statistical power (Fig. 5). We expected that any impact from trawling would be most pronounced in this study after high-intensity trawling was conducted a year later at the same study plots; however, the trajectories of the differences in microtopographic complexity at the control and trawled plots were even less clear than those for plots where low-intensity trawling was conducted, converging at 2 weeks after trawling, increasing while diverging significantly at 6 months, and then converging again at 1 year after trawling.

Insofar as our trawling activities represented a type-I disturbance, where a relatively small disturbed area is surrounded on one or more sides by undisturbed habitats or organisms (Connell and Keough, 1985), it is possible that the lack of a significant impact to microtopographic structure on the seafloor resulted from the rapid colonization of the patches by bioturbating organisms from surrounding areas. This colonization may also explain why the temporal variation in the data was more pronounced than the spatial variation. Despite the minimal reduction in microtopographic complexity observed in the trawled plots, we did find, on a larger scale, alteration of the seafloor in the form of scour marks from trawl doors that were visible immediately after both low- and high-intensity trawling and that persisted for up to a year after low-intensity trawling.

The persistence of these tracks is not without precedent (Friedlander et al., 1999), yet the ecological effects of these scour marks, which we estimated to be up to 20 cm wide and 10 cm deep and to extend for many meters, are not known. Still, scour marks do represent an alteration of the seafloor. They could positively affect organisms through mobilization of key prey items (Shephard et al., 2009) or creation of additional habitat structure (Kaiser and Spencer, 1994). Conversely, the scour marks could negatively affect organisms depending on the nature and extent of their association with the seafloor and the substrate type.

Our expectations also were not borne out with respect to densities of sessile, structure-forming macroinvertebrates. Biogenic structures on the seafloor have been shown to be important for demersal and benthic fishes at multiple life history stages (Baillon et al., 2012; Auster et al., 2003a). However, in our study, there were no significant differences between control and trawled plots with respect to densities of sessile macroinvertebrates, which were already at relatively low densities at the start of the study. Further, the densities of mobile invertebrates varied considerably over the course of our study but did not differ significantly between levels observed at control and trawled plots with either low- or high-intensity trawling effort. A brief investigation of infaunal organisms conducted as part of this study (Kitaguchi, 2011) also revealed no differences.

Most of the invertebrate groups that we assessed had low densities but showed high spatial and temporal variability. Polychaete worms and ophiuroids were especially patchy and variable in their distributions. Information on the dynamics of organisms in and on unconsolidated sediments of the outer continental shelf off the central California coast continues to be very limited, despite the fact that unconsolidated sediments characterize more than 80% of the continental shelf in California (Allen et al., 2006). Indeed, the dominant characterization of communities on soft sediments worldwide has been one of patchiness at multiple scales (Morrisey et al., 1992; Oliver et al., 2011), where the distributions of organisms are frequently more diffuse than the distributions of species associated with shallow-water reefs where habitats are more discrete.

With this considerable variability as a backdrop, we detected no anthropogenic impact from bottom trawling despite the precisely georeferenced trawling effort and post-trawling ROV surveys. However, we expect that the time series data on invertebrate communities (both sessile and mobile) collected as part of this project will ultimately enhance our understanding of the ecology of organisms in unconsolidated sediments, including seasonal and interannual variability in the distribution of mobile and epibenthic invertebrates, the patchiness of opportunistic organisms, and interannual variability in invertebrate community structure.

The results of any field research project, as well as the implications of those results, must ultimately be contextualized by a variety of factors. We planned statistical analyses to maximize our chances to capture moderate-to-large effects on trawling metrics. This relatively high statistical power strongly indicates that moderate to large impacts to the metrics that we analyzed would have been detected if they had occurred. However, the very limited impacts of bottom trawling to the seafloor that we observed must be considered in light of 2 primary factors: the use of a small-footrope bottom and the location of the study area in unconsolidated sand sediments.

The small-footrope gear was used at 2 distinct trawling intensities (3 and 8 times per trawled plot) that were designed to reflect the low to moderate intensity trawling historically seen in the region off central California (Mason et al., 2012). Yet, with the heterogeneous distribution of trawling effort among fishing vessels, and more specifically, regular focusing of that effort on favored locations that differ among captains, some areas of the seafloor may be impacted more intensively (Auster et al., 1996; Mason et al., 2012). Additionally, much of the historic effort (trawling before the implementation of the federal requirement for small-footrope gear along the continental shelf in 2000) in the study area was prosecuted with a variety of bottom trawls, most of them likely employing larger footrope gear and heavier trawl doors than those on the bottom trawls that we used in our study. As such, the required small-footrope gear may cause less impact than heavier gear, and therefore the extent to which the lack of impacts that we observed can be extrapolated to other gear types is potentially limited.

Substrate type is also an important factor that must be considered in any extrapolation of the results of our study, as is the behavior of the organisms found in the study area. Our study was located on the outer continental shelf in an area characterized by low-relief, unconsolidated sandy sediments of relatively low diversity (Oliver et al., 2011). We considered the area to be broadly representative of the shelf to the north and south of the study area on the basis of preliminary exploratory surveys completed before this study began and on the basis of additional research that we completed elsewhere along the coast. The additional reference sites that we sampled in May 2012 (Fig. 1) appeared to be similar to the study area with respect to the percent cover of microtopographic features (Fig. 4A). However, the density of sessile invertebrates was higher at the north reference site (Fig. 4B), and the density of mobile invertebrates was higher at both reference sites compared with results in the study area (Fig. 4C). Again, the patchiness in the distribution of organisms on the continental shelf may explain these differences, and organism responses to trawling may also play a role. A study by Troffe et al. (2005) suggested that sea whips of the same genus observed in our study may have the ability to rebound after being knocked over by a passing bottom trawl; however,

Malecha and Stone (2009) found that recovery of sea whips damaged by trawling was limited.

We focused on the potential impacts of bottom trawling with small-footrope gear on fish habitat on the seafloor off central California. In the context of ongoing efforts to understand and manage fishing impacts (Dinmore et al., 2003; Hannah, 2003; Bellman et al., 2005; Ellis et al., 2008; Hourigan, 2009; de Juan and Lleonart, 2010), the results of our study indicate that bottom trawling with small-footrope gear may have limited impacts in sandy habitats of the outer continental shelf in California. Although the global literature clearly indicates that communities on hard substrates are more vulnerable to bottom trawling (see reviews in Dayton et al., 1995; Kaiser et al., 1998; Watling and Norse, 1998; NRC, 2002; Barnes and Thomas, 2005), the lack of impacts to unconsolidated sandy sediments at a depth of 170 m as observed in this study indicates that this type of sediment is much less vulnerable, at least at the level of fishing effort undertaken for this study with a bottom trawl that met the federal requirement of a small footrope (≤20 cm in diameter). Identification of habitats and depth zones appropriate for bottom trawling in the "working seascape" among closed areas will be important for efforts to balance regulations of local seafood and fish landings and the needs of fishermen's livelihoods with environmental impacts of trawling across the continental shelf and slope habitats.

Acknowledgments

Generous support for this project was provided by the California Ocean Protection Council through a State Coastal Conservancy Grant to The Nature Conservancy (SCC grant no. 10-058), private donations from the Kabcenell Family Foundation and the Seaver Institute, and contributions from the James W. Rote Professorship and the Undergraduate Research Opportunities Center at California State University Monterey Bay. We thank the many students who participated throughout this study (including J. Derbonne, who passed away before the completion of the project). For key support in the field, we recognize the captains and crews of the FV *Donna Kathleen*, FV *South Bay*, and RV *Fulmar* and the ROV team from Marine Applied Research and Exploration. We also thank staff from NOAA Fisheries, the West Coast Groundfish Observer Program, and the Morro Bay Harbormaster's Office. Suggestions provided by 3 anonymous reviewers improved the manuscript.

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General text must be typed in 12-point Times New Roman font throughout. A brief introduction should convey the broad significance of the paper; the remainder of the paper should be divided into the following sections: **Materials and methods, Results, Discussion**, and **Acknowledgments**. Headings within each section must be short, reflect a logical sequence, and follow the rules of subdivision (i.e., there can be no subdivision without at least two subheadings). The entire text should be intelligible to interdisciplinary readers; therefore, all acronyms, abbreviations, and technical terms should be written out in full the first time they are mentioned.

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Dates should be written as follows: 11 November 2000. Measurements should be expressed in metric units, e.g., 58 metric tons (t); if other units of measurement are used, please make this fact explicit to the reader. Use numerals, not words, to express whole and decimal numbers in the general text, tables, and figure captions (except at the beginning of a sentence). For example: We considered 3 hypotheses. We collected 7 samples in this location. Use American spelling. Refrain from using the shorthand slash (/), an ambiguous symbol, in the general text.

Word usage and grammar that may be useful are the following:

- *Aging* For our journal the word *aging* is used to mean both age determination and the aging process (senescence). The author should make clear which meaning is intended where ambiguity may arise.
- *Fish and fishes* For papers on taxonomy and biodiversity, the plural of *fish* is *fishes,* by convention. In all other instances, the plural is *fish.*

  Examples:

  The fishes of Puget Sound [biodiversity is indicated];

  The number of fish caught that season [no emphasis on biodiversity];

  The fish were caught in trawl nets [no emphasis on biodiversity].

  The same logic applies to the use of the words *crab* and *crabs, squid* and *squids,* etc.
- *Sex* For the meaning of male and female, use the word *sex*, not *gender.*
- *Participles* As adjectives, participles must modify a specific noun or pronoun and make sense with that noun or pronoun.

  Incorrect:

  Using the recruitment model, estimates of age-1 recruitment were determined. [Estimates did not use the recruitment model.]

  Correct:

  Using the recruitment model, we determined age-1 estimates of recruitment. [The participle now

modifies the word *we,* those who were using the model.]

Incorrect:

Based on the collected data, we concluded that the mortality rate for these fish had increased. [*We* were not based on the collected data.]

Correct:

We concluded on the basis of the collected data that the mortality rate for these fish had increased. [Eliminate the participle and replace it with an adverbial phrase.]

Equations and mathematical symbols should be set from a standard mathematical program (MathType) or tool (Equation Editor in MS Word). LaTex is acceptable for more advanced computations. For mathematical symbols in the general text (α, χ^2, π, $\pm$, etc.), use the symbols provided by the MS Word program and italicize all variables. Do not use photo mode when creating these symbols in the general text.

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